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MR448: Bees and Their Habitats in Four New England States

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Bumble bees on butterfly milkweed, Asclepias tuberosa, Blue Hill, Maine, July 25, 2013. Photo by A.C. Dibble

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ABSTRACT

Four states contain over 401 species of bees, about which little is known except for a few common species. Forests of Maine, Massachusetts, New Hampshire, and Vermont were largely cleared in colonial times, then trees grew back as of the 1870s. Canopy closure, urbanization, and intensive agriculture have led to reduced habitats for bees. Managed and wild bees of the region are found especially in forest openings. Many visit flowers across different plant species, though an estimated 15% visit only one or a few plant taxa. Because bee life histories, population dynamics, and host plant relations are incompletely known, an emphasis on habitat is appropriate because the environment can be manipulated. We list 15 bee habitats with natural and anthropogenic features, and suggest 40 plant taxa that may be effective in plantings for bees. Pollination systems in two native crops, lowbush blueberry (*Vaccinium angustifolium*) and cranberry (*V. macrocarpon*), are better-studied than most crops; from these we developed an economic perspective on altering habitat to support bees. Threats to bees include habitat loss, pests and pathogens, pesticides, and climate change. We consider practical aspects for improving pollinator habitats. The adoption of suggested habitat improvements will help meet goals in bee conservation and pollination security, and could aid in protecting pollination of the native flora. We identify gaps in knowledge to help prioritize future research directions.

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INTRODUCTION

Bees are crucial to pollination in unmanaged ecosystems and some crops, and their roles are increasingly understood in four states in the Northeastern U.S., abbreviated "NNE" in this paper: Maine (ME), Massachusetts (MA), New Hampshire (NH), and Vermont (VT). The four states have in common many native bee and plant species, forest types, and natural communities. They share drought events and risk of wildfire (Irland 2013). They are exposed to many of the same major storms (e.g., hurricanes, Foster 1988), pollution events (Hand et al. 2014), and effects ascribed to climate change (Hayhoe et al. 2008). Beekeeping enterprises (the western honey bee, *Apis mellifera*, an introduced species) of various sizes exist in each of the states. By including the four states in this review, we hope to better understand wild bee distributions, inspire the expansion of floral resources to support bee populations in a strategic manner, reduce use of pesticides, create pollinator corridors, and protect subtle habitat features such as ground nest sites for solitary bees and patches of native vegetation that are free of invasive plants.

We focus on bees — both wild (mostly native) and managed (mostly not native) — because they are the most effective pollinators in our region, and have importance for crops in NNE. Wild bees differ from honey bees in that wild bees are resident without management in a given locale, while honey bees are usually managed in hives. Other kinds of managed bees are also used in NNE and are reviewed in some detail below. Wild bees in NNE include a few adventive (non-native but arrived without purposeful introduction) species (i.e., *Andrena wilkella* and *Lasioglossum leucozonium* [Giles and Ascher 2006]) but for purposes of this discussion, do not include feral honey bee colonies. Wild and managed bees can synergistically interact (Greenleaf and Kremen 2006, Brittain et al. 2013) or alternatively, compete (Thomson 2004), though there has only been one such study that we are aware of in NNE (Drummond 2016). This review might appear to favor the topic of managing pollinators for the sake of crops, but wherever possible we sought to address bee biodiversity. Pollinating non-bee insects such as butterflies, moths, flies, and beetles (Rader et al. 2015), plus hummingbirds, bats, and other animals, are components of biodiversity, but their contributions to pollination are lower for crops grown in NNE. Space limitations here prevent coverage of non-bee pollinators.

The value of bees to people has been estimated at global and nation-wide scales in the U.S. Globally an estimated 90% of flowering plant species benefit from animal-mediated pollination (Ollerton et al. 2011). Both managed and wild bees have vast importance for food security because of their role as pollinators of many crops. An estimated one-tenth of the value of global food production is attributable to insect pollinators (Gallai et al. 2009). In the U.S., during the late-1990s, honey bees contributed an estimated $21.87 billion of total U.S. crop production value (Morse and Calderone 2000), though other estimates are lower (Southwick and Southwick 1992). On a global basis, wild bees are estimated to contribute more to pollination than honey bees (Garibaldi et al. 2013). Another estimate of the value of wild bee pollination services (Koh et al. 2015) suggests that in 2009, bees (commercial honey bees + wild bees) contributed an estimated $14.6 billion per year in the U.S. Of this at least 20% ($3.07 billion) was provided by wild bees. These estimates are difficult to verify, but they suggest that wild bees contribute greatly to the U.S. economy in the range of $3-14 billion or more. More regionally, in ME, wild bees are important in providing pollination services to lowbush blueberry (*Vaccinium angustifolium*). Asare et al. (2017) showed in an 11-year study that 30-50% of pollination was due to wild bees. The lowbush blueberry crop depends on bee pollination. The flowers have sticky pollen in poricidal (tube-like) anthers, and most effective pollination occurs by bumble bees and some *Andrena* species which rapidly vibrate their flight muscles (sonication, or buzz pollination) to shake pollen loose from within the anthers (Bell et al. 2009). Honey bees do not sonicate, and they are commonly attracted away from the crop by flowers with more accessible rewards, yet crop yields are sufficient if honey bees are present at high density during flowering (additional aspects covered below). In 2007 direct and indirect economic impact of the lowbush blueberry production system in ME totaled $250 million (Yarborough 2009). Therefore, it might be expected that in the absence of honey bee pollination (i.e., if honey bees were not rented and brought into ME for this crop), wild bees would contribute between $75-125 million dollars to the state economy (Yarborough 2009).

Attention to bees and their habitats in NNE is on the rise in recent decades due in part to a crisis in honey bee sustainability called Colony Collapse Disorder (CCD), a hive loss syndrome (further details below). Accompanying this interest is increased funding for research, public outreach and pollinator-focused agricultural programs. As of the Farm Bill of 2008, NNE growers have applied to the U.S. Department of Agriculture through the Natural Resources Conservation Service (NRCS), which partners with the nonprofit Xerces Society for Invertebrate Conservation (hereafter "Xerces") for technical expertise and financial incentives in the form of cost-share assistance to plan and undertake conservation practices that enhance pollinator habitat on farms. State agencies, conservation organizations, and Cooperative Extension educate the public regarding pollinator conservation (Stubbs et al. 1996, Stubbs et al. 2000, Drummond 2015, Venturini et al. 2017a). All of these avenues, and more, have contributed to public interest and altered attitudes toward bees and their habitats over recent years in NNE.

With the decline of honey bees, there is concern that wild bees could also be in decline. Data are insufficient to assess population trends for most or all wild bee species in NNE, though methods for surveying bees have improved since Procter (1946). The diversity and abundance of wild bees vary considerably from location to location in the region (MacKenzie and Averill 1995, Stubbs et al. 2008, Notestine 2010, Droege 2012, Bushmann and Drummond 2015, Goldstein and Ascher 2016). Surveys of wild bees typically result in a high proportion of singleton species (observed only once), with a high incidence of rare (within that dataset) species (Russo et al. 2015). Insufficient data exist to assess population trends for most or all wild bee species in NNE, though the relative abundance of species can be compared from one year to the next. Communities are highly variable and have been shown to fluctuate yearly in both abundance and species richness over a three-year period in lowbush blueberry ecosystems (Bushmann and Drummond 2015, Drummond et al. 2017). Over a 29 year period at a single blueberry field in ME the wild bee community varied widely, but did not show a trend suggesting decline (Drummond et al. 2017).

Bumble bees have attracted the most conservation attention in northern temperate climates. Globally, multiple species of bumble bees have declined in observations and collections throughout their range (Goulson et al. 2008, Cameron et al. 2011, Bushmann et al. 2012, Colla et al. 2012, Bartomeus et al. 2013a, Williams et al. 2014). A recent summary of *Bombus* captures on cranberry (*Vaccinium macrocarpon*) flowers in MA reported that at least half of the species previously observed in the region have become very rare or locally extinct (Averill et al. in press). In 2017 the U.S. Fish and Wildlife Service listed *B. affinis,* the rusty-patched bumble bee, as endangered under the Endangered Species Act; this was the first application of the Act for a bumble bee species, though seven species of *Hylaeus* from Hawaii were listed in 2016. Some bumble bees of NNE are currently on the Red List of the International Union for the Conservation of Nature (IUCN 2016): *Bombus affinis* was recognized as critically endangered, *B. terricola* (Figs. 1a, c) and *B. pensylvanicus* as vulnerable and decreasing, and *B. ashtoni* (syn. *Bombus bohemicus* by some authors, e.g., Williams et al. 2014) and *B. fervidus* as declining with data deficient. In apparent decline by IUCN criteria are two additional cuckoo bees of NNE, *B. fernaldae* and *B. insularis*. At the state level, ME recognized 10 species of *Bombus* in the 2015 State Wildlife Action Plan as Species of Greatest Conservation Need (Whitcomb and Additon 2015). Of these, *B. affinis* is Level 1 or top priority; *B. ashtoni, B. pensylvanicus* and *B. insularis* are Level 2; and *B. citrinus, B. fernaldae, B. fervidus, B. griseocollis,* and *B. terricola* are Level 3. Vermont under its state endangered species law listed three species in 2015: *B. affinis, B. terricola,* and *B. ashtoni*. Xerces lists *B. affinis* as 'imperiled' in MA, ME, NH, and VT, and the yellow-banded bumble bee, *B. terricola*, as 'imperiled' in MA, ME, NH, and VT. Recent data from numerous sites in ME suggest a resurgence of *B. terricola* (Figure 1c) in that state (F.A. Drummond, unpublished data). Some wild bee species appear to be increasing in recent decades (e.g., the tri-colored bumble bee, *Bombus ternarius*, in ME, Figure 1b), but many others are apparently declining (Bushmann et al. 2012, citizen science surveys in VT and ME, see http://val.vtecostudies.org/projects/bumble-bee-atlas/ and http://mainebumblebeeatlas.umf.maine.edu/). Some bumble bee species might have been rare for millenia, so their rarity and limited distribution could be consistent with their history. Volunteers engaged in citizen science activities have wondered if collecting bees for expert identification harms populations. Monitoring techniques developed by Droege et al. (2010), which involve passive but mortal capture of bees, are in wide

use and could eventually reveal patterns of stability and decline in bee species richness, or within a species. Other than a relatively few species, status is unknown for most of the 401 wild bee species in NNE, so this information could improve the effectiveness of management for conservation. For most wild bees, collection of voucher specimens to document bee diversity and abundance is unlikely to threaten populations because the insects are short-lived and have relatively high fecundity. The data obtained from physical specimens is superior to that from photographic evidence because features on a specimen examined in the microscope are not available in most photos. However, with listing of *Bombus affinis* as federally endangered, there will be increased use of photography and further evaluation of collecting methodology so as to not inadvertently impact its rare populations.

Because documentation of population dynamics for one bee species at a time is difficult, and bee communities (multiple species in one place) fluctuate widely from one year to the next, the emphasis in bee conservation can be placed on threat assessment and habitat improvement. Threats attributed to habitat loss, pesticides, pests and pathogens, and climate change can be measured and monitored. Additions of floral resource habitat and other improvements have been shown to increase bee abundance and diversity, and to increase the stability of these over time. Such additions can increase pollination services in nearby crop fields (Morandin and Kremen 2013, Wood et al. 2015, Pywell et al. 2015, Venturini et al. 2017b).

Bee habitat consists especially of the type and abundance of food resources, or flowers from which bees obtain nectar and pollen. Bees also require sufficient nest sites and overwintering habitat, which are necessary for the animals to complete their life cycles. These elements are often patchily distributed through a landscape, and might be compromised by changes such as forest succession that leads to closed canopy shade conditions, or climate change-related patterns that lead to increased number of rainy days in spring during which bees are unlikely to fly (Drummond et al. 2017a). Consideration must be given to habitat connectivity and landscape context, quality of forage (e.g., invasive plants might not provide sufficient nutrition or a succession of flowers), and exposure to pesticides. Less-recognized as habitat aspects are inter- and intra-specific interactions with other pollinators or with associated species such as cuckoo bees, pests and pathogens. Some of the aspects mentioned here cannot be manipulated easily. Regarding habitat improvements, greatest emphasis in NNE is on (1) increasing the area in plantings to provide more flowers, and (2) reducing pesticide use.

Our objective in this review is to synthesize from a conservation standpoint the state of knowledge regarding bees in NNE, including their diversity, and biology especially as it relates to climate change. We review foraging and nutrition, nest ecology, parasites and parasitoids, native vs. managed bees, and interactions with plants. We then turn our focus to bee habitats, and identify 15 habitat types we find useful for recognizing essential bee resources. We discuss habitat aspects including forest succession, invasive plants, land use alterations, and agriculture including impacts of pesticides, and cover economic aspects of crop-related pollination reservoirs in NNE that demonstrate cost-effectiveness at various scales. We present habitat improvement strategies including passive and active approaches, based on the literature and our experiences in NNE, and we suggest plants for pollinator plantings. Wherever pertinent throughout the text, we highlight threats to bees in our region such as pests and pathogens, pesticides, and habitat loss. Finally, we identify gaps in knowledge that could help in prioritizing directions for future research. We hope this review will be useful to anyone seeking to protect bees and their habitats.

THE BEES

Diversity and bee families

In NNE 401 wild bee species have been recorded in six families: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae (this family is included by some authors in the Apidae) and 39 genera (Ascher and Pickering 2016). We know of no bee species found only in NNE and not elsewhere; all are apparently distributed outside the four states also. Some examples of bees that have been documented in all four states are in Table 1, and a few are illustrated in Figure 1 (a-h). Wild bees range in size from bumble bee queens that are noticeable in the spring, to somewhat obscure and tiny *Lasioglossum* species (sweat bees). Bee species richness

by state for MA, ME, NH and VT is only partly known. A bee checklist would ideally reflect total number of known native and non-native bee species, but for some counties in most of these states, few or no surveys have been undertaken. In ME, 277 species of bees have been documented. Of these, all but six or seven are native, but only four of the 16 counties have been surveyed extensively (state checklist by county, Dibble et al. 2017). MA has 377 bee species (Goldstein and Ascher 2016), NH has 118 species from five families and 24 genera documented by Tucker and Rehan (2016), and VT has 270 species (Ascher and Pickering 2016). Loose et al. (2005) found up to 80 species associated with MA cranberry agroecosystems and Averill et al. (in press) documented 72 species foraging on cranberry flowers. Bushmann and Drummond (2015) found more than 120 species associated with ME lowbush blueberry agroecosystems. In all cases, additional species are likely to be added. Nonnative bees that are documented in ME and thought to be likely in all four states include *Apis mellifera* (feral colonies), *Megachile sculpturalis*, *Lasioglossum leucozonium, Anthidium manicatum* (Figure 1d), and *Andrena wilkella*.

The family Andrenidae is represented by six genera in NNE: *Andrena* (Figure 1e), *Calliopsis*, *Panurginus*, *Perdita, Protandrena,* and *Pseudopanurgus* (USDA-NRCS, 2009). Bees in the genus *Andrena* are the sand bees or mining bees and are species-rich in NNE, with 53 species in ME alone based on vouchered county-level data (Dibble et al. 2017), and about 90 species in NNE. The Andrenidae are solitary, ground-nesting bees, many of which are active during spring. Some of the Andrenidae have importance as pollinators of a major fruit crop in ME, lowbush blueberry (Stubbs et al. 1992, Bushmann and Drummond 2015, Drummond 2016, Venturini et al. 2017c). Thirteen of 50 *Andrena* species found in lowbush blueberry in ME are also found in cranberry in MA in mid-late June, though in low numbers (MacKenzie and Averill 1995, Loose et al. 2005). Among spring Andrenidae are *Andrena bradleyi* and *A. carolina*, which are common in NNE and visit flowers of plants in the Ericaceae (Stubbs et al. 1992, Bushmann and Drummond 2015, Fowler 2016). Other examples of Andrenidae include *Andrena asteris, A. placata,* and *A. nubecula* (all common in NNE); these appear to be summer species and are often collected on goldenrods (*Solidago* spp.) (Fowler 2016).

The family Apidae consists of 14 genera in New England alone. These are *Anthophora, Apis, Bombus, Ceratina* (Figure 1f), *Epeoloides, Epeolus, Habropoda, Holcopasites, Melissodes, Nomada, Peponapis, Svastra, Triepeolus,* and *Xylocopa* (Michener 2007). There are 19 species of bumble bees native to the six New England states (Colla et al. 2011, Bushmann et al. 2012, Williams et al. 2014, Bushmann and Drummond 2015). Of these, five are in the subgenus *Psithyrus*, and are cuckoo bumble bees that parasitize the nests of other bumble bee species. Bumble bees are eusocial (that is, social and often with a single reproductive female, the gyne, though bumble bee workers often lay their own eggs) and in NNE, they are active from March/April into October. North American bumble bee species are all pollen generalists, though individuals within a colony show varying degrees of specialization (Heinrich 1976, Woodgate et al. 2016).

The Colletidae includes two genera (*Colletes* and *Hylaeus*) native to NNE (USDA-NRCS 2009). Of these, *Hylaeus* (the yellow-faced bees) are found throughout the growing season, while *Colletes* (plasterer or polyester bees, Figure 2a, 2b) are mostly early in the season, with some species active in autumn when goldenrod is in flower.

The Halictidae contains eight genera native to NNE. These are *Agapostemon, Augochlora* (Figure 1g), *Augochlorella, Augochloropsis, Dufourea, Halictus, Lasioglossum,* and *Sphecodes*. Of these, in NNE *Lasioglossum* contains the most species (USDA-NRCS 2009). Most Halictidae are generalists and solitary ground nesters, but a few are social in NNE. *Lasioglossum nelumbonis* forages on flowers of aquatic plants and also of upland plants, and was observed in ME in a blueberry field adjacent to a wetland (Bushmann 2013).

The Megachilidae includes eleven genera found in NNE. These are *Anthidiellum, Anthidium, Chelostoma, Coelioxys, Dianthidium, Heriades, Hoplitis, Megachile* (Figure1h), *Osmia, Paranthidium,* and *Stelis*. *Osmia* are the mason bees, and *Megachile* are the leaf cutter bees; both genera are mostly active in spring though some species are active in summer (USDA-NRCS 2009).

The Melittidae contains two genera (*Macropis* and *Melitta*) in NNE (USDA-NRCS 2009). These uncommon to rare summer-active bees are specialists on just a few plant groups (Fowler 2016). *Macropis* forages on loosestrife, *Lysimachia* spp., and *Melitta* upon

blueberries/cranberries (*Vaccinium* spp.) or maleberry (*Lyonia ligustrina)*.

Bee biology and distribution as they relate to climate in NNE

Basic information regarding bee biology can be readily found (e.g., Michener 2007). For this paper, we sought patterns that might differ in NNE from elsewhere within the range of a bee species. Several Halictidae species that are common in NNE have been shown elsewhere to have either latitudinal or altitudinal shifts in their sociality and phenology: these examples are *Augochlorella striata* (Packer 1990) and *Halictus rubicundus* (Eickwort et al. 1996). As climate change proceeds there could be an increase in frequency or intensity of such behavioral shifts.

These and other (mostly) solitary bees of NNE tend to emerge in synchrony with their host plants. Some are oligolectic and their active period coincides with availability of floral resources needed for their brood (Danforth 2007). Timing of the emergence of ground nesting bees is temperature-related, whereas flowering of bee host plants probably has more to do with day length (Pywell et al. 2006). In a scenario of climate change in NNE, there is concern of increasing lack of synchrony in the phenology of plants and bees. This was suggested by Miller-Rushing and Primack (2008) based on a study of the first day of flowering for 43 spring-flowering plants observed from 1852-1858 by Henry David Thoreau in MA, by Alfred Hosmer (1888-1902), and by the authors (2004-2006). The last set of dates were seven days earlier than in Thoreau's time. Fowler (2016) pointed out the needs of specialist bees, some of which might be the first to be affected by asynchrony of flowering in NNE. In the western U.S., the indirect effect of climate change in altering flowering plant phenology with sub-alpine bumble bee emergence and need for resources was shown to be a significant phenomenon driving the inter-annual fluctuation of bumble bee abundance (Ogilvie et al. 2017). Another indirect effect of climate change on bees might be increased CO_2 levels in the atmosphere. Ziska et al. (2016) showed that increased CO_2 reduced the protein content of pollen in Canada goldenrod (*S. canadensis)* grown under enriched conditions. The authors suggest that this could be detrimental to bees in the future.

Climate warming is well-documented in NNE. Frumhoff et al. (2007) summarized the Northeast (including but not exclusive to MA, ME, NH and VT) as warming at almost 0.28°C each decade, with winter temperatures increasing at a rate of 0.72°C per decade from 1970-2000. With this has come more days with temperatures above 32°C, a longer growing season, increased precipitation with a higher proportion of it falling as rain, less snowpack and greater snow density, earlier ice-out on lakes and rivers, rising sea-surface temperatures and rising sea levels. These trends continue in NNE. The latest analysis of climate in the Northeast for 2017 (NOAA 2017) shows that the summer was cooler overall (-0.56°C), wetter in spring and early summer (107% of normal), and extremely dry in the late summer (drought conditions prevailed in 13% of Northeastern states).

The influence of climate upon distributions of bees suggests that species are undergoing a change in range area. The recent spread of two nonnative bees in NNE, the giant resin bee (*Megachile sculpturalis*) and the wool-carder bee (*Anthidium manicatum*), implies potential for changing distributions for other bee species also (Dibble et al. 2017). For other bee species, the change is negative. Kerr et al. (2015) found that bumble bees in Europe and North America are retreating from the southern extremes of their ranges, but not expanding northward. This retraction is due to warming, but there is no reciprocal expansion to the north and not a clear reason why. Some bumble bee populations are moving upslope in response to climate warming.

Too much rain can affect bees, as they are most active during dry, sunny conditions, they are thought to navigate at least in part by the sun, they land upon dry flowers where an electric charge is part of the attraction (Clarke et al. 2013), and they consume pollen from dry anthers. If the flowers are wet, then fewer bees are likely to fly or gather necessary food resources until conditions meet their needs. For a given bee species, an unknown threshold number of flight days is required to provision its brood; if flight days are reduced, then fewer offspring may be successful. Number of flight days over four decades in Hancock County, ME has decreased with wetter weather in spring (Drummond et al. 2017). Wet soil may increase the loss of diapause pupae and adults when fungi attack and poor conditions prevail. We found no record that increased fungal disease in bees is yet documented in NNE.

Drought can also be problematic for bees as nectar flow decreases in drought conditions (LeConte and

Table 1. Examples of apparently common bee genera or species documented in most or all four northern New England states, their families, and noteworthy aspects for each. "*" =nonnative bees in our region. Sources: MacKenzie and Averill (1995), Bushmann and Drummond (2015), Goldstein and Ascher (2016), Tucker and Rehan (2016), Ascher and Pickering (2016), Dibble et al. (2017).

Bee species	Family	Noteworthy aspects
**Apis mellifera*	Apidae	Not native to North America, feral populations in decline
Agapostemon virescens	Halictidae	Metallic green thorax, black and white striped abdomen
Augochlorella aurata	Halictidae	Metallic body
Halictus rubicundus	Halictidae	Sweat bee, brown
Halictus confusus confusus	Halictidae	Sweat bee, brown
Lasioglossum admirandum	Halictidae	Sweat bee
Lasioglossum acuminatum	Halictidae	Sweat bee
Hylaeus annulatus	Colletidae	Yellow-faced bee
Ceratina dupla	Apidae	Tiny carpenter bee, nests in pithy stem
Ceratina calcarata	Apidae	Tiny carpenter bee, nests in pithy stem
Andrena dunningi	Andrenidae	Solitary ground-nesting bee
Andrena carlini	Andrenidae	Solitary ground-nesting bee
Andrena crataegi	Andrenidae	Solitary ground-nesting bee
**Lasioglossum leucozonium*	Halictidae	Not native to North America
**Andrena wilkella*	Andrenidae	Not native to North America
Osmia atriventris	Megachilidae	Leaf cutter bee
Osmia pumila	Megachilidae	Leaf cutter bee
Megachile inermis	Megachilidae	Mason bee
Xylocopa virginica	Apidae	Native carpenter bee, makes tunnels in wood
Bombus impatiens	Apidae	Native populations and also introduced in commercial quads
Bombus ternarius	Apidae	Common, apparently stable populations in the region
Bombus vagans vagans	Apidae	Common
Nomada cressonii	Apidae	Kleptoparasite on *Andrena*
Nomada luteoloides	Apidae	Kleptoparasite on *Andrena*
Peponapis pruinosa	Apidae	Can be found in flowers of squashes, pumpkins, active early a.m.
**Anthidium manicatum*	Megachilidae	Not native to North America
Colletes inaequalis	Colletidae	Active in spring, lines nest with a waterproof substance

Navajas 2008). Drought in 2016 in parts of NNE led to possible low flow of nectar and pollen (not measured). Moffett and Parker (1953) and Rashad and Parker (1958) have shown that in Kansas, nectar flow and pollen production both fall during drought. In NNE, the 2016 drought was followed by a perceived low abundance of wild bees in spring 2017 concurrent with cool, wet weather in March-May, and drought again in late summer 2017 (A.C. Dibble, personal observation). If multiple growing seasons reflect such conditions year after year, the concern is that wild bees will be unable to maintain robust populations. Rashad and Parker (1958) found this to be the case for honey bees in which decline of bee populations occurred after three continuous years of drought in Kansas.

Foraging and nutrition

Specialization of bees upon just a few plant species (oligolecty) has been estimated at about 15% of bee species in New England (Fowler 2016). For example, bees in the family Melittidae exhibit oligolecty (Michez and Patiny 2005). Most common bee species of NNE are wide-ranging in their floral visitation patterns and are not limited to one species, genus, or even family of

plants; they behave as opportunists with a wide niche and they gather pollen and nectar from various unrelated plant species (polylecty) (Eickwort and Ginsberg 1980). The majority of NNE plants are thought to be not wholly dependent on any one bee species. In NNE bee gardens, plant selection that favors the specialists will likely meet needs of generalist bees also (Fowler 2016).

Most bees in NNE clearly favor flowers of some plant species over those of others (e.g., Bushmann and Drummond 2015; Venturini 2015, Venturini et al. 2017b). Researchers have sought to explain selective foraging by floral density, color, morphology, fragrance, sugar content in nectar, and other aspects of nutritional quality (Somme et al. 2015, Ruedenauer et al. 2016, Vaudo et al. 2016). Many pollinators can rapidly associate several flower characteristics with food rewards, including floral color combinations (Wilbert et al. 1997, Wesselingh and Arnold 2000), fragrance (Knudsen et al. 2001, Raguso 2008), and size and shape of flowers or inflorescences (Møller and Sorci 1998, Spaethe et al. 2001, Whitney and Glover 2007, Wignall et al. 2006).

Study of nutritional aspects of floral resources has been undertaken largely outside NNE, with over arching trends that can be assumed to apply to NNE bees. Bee diets that are high in nutritional content have been linked to higher fitness, foraging ability, and body size in some species (Roulston and Cane 2002, Burkle and Irwin 2009, Couvillon et al. 2011, Vanderplanck et al. 2014, Lawson et al. 2016, Moerman et al. 2016). Data from NNE include secondary metabolites in nectar of turtlehead (*Chelone glabra*) by Richardson and Irwin (2015) and by Richardson et al. (2016). Additional reports are in development (A. White with data from VT, M. Leach with data from ME).

Wild versus managed bees on crops in NNE

Presence of bees — whether wild or managed — during flowering of some NNE crops is essential, especially for highbush blueberry, lowbush blueberry, raspberry, cranberry, apple, squash, and pumpkin. Bee-visited flowers result in fruits that are larger, more marketable, and seed set is greater (Delaplane and Mayer 2000). Additional food crops grown in NNE that produce higher yields when bees have access to their flowers are strawberry and watermelon. Seed crops for culinary and medicinal herbs and for seed mixes for wildflower meadows are examples of crops in NNE that are not well-quantified but depend on bee pollination.

Some bee species are particularly important crop pollinators in NNE (e.g., bumble bees), while other wild bee species might visit crop flowers but have a negligible effect on pollination (e.g., some sweat bees, yellow-faced bees, and cuckoo bees that have few hairs on their bodies). The most important bees found to visit lowbush blueberry are *Andrena* spp. (e.g., *A. carlini, A. carolina,* and *A. vicina*) (Bushmann and Drummond 2015), and *Bombus* spp. (e.g., *B. ternarius, B. impatiens, B. bimaculatus*) (Javorek et al. 2002). In the cranberry agroecosystem in MA, where bumble bees are the most efficient pollinators, workers of *B. impatiens*, *B. griseocollis*, *B. perplexus*, and *B. bimaculatus* are by far the most abundant species (Averill et al., in press).

The relative abundances of wild versus managed bees (esp. honey bees) in NNE is not known. A survey in the late 1950s (Morse 1960) was an early attempt to relate abundances of these two categories and included surveys in MA, NH, VT, and NY (not ME). We could find no comparison study conducted in recent times. There are many differences between wild bees and honey bees, with implications for pollinator effectiveness. Honey bees were brought to North America by European colonists and were known in Jamestown, Virginia in 1621 (Buchmann and Nabhan 1996). Each honey bee hive has an estimated 50,000 honey bee workers per colony, although only 20-25% are foragers. By contrast, a large bumble bee nest has about 200 individuals, of which almost all are foragers. Honey bees can forage up to about 5 km from the hive, while a small wild bee might forage within just 100 m of its nest, though bumble bees can go much farther. Honey bees can be brought to the crop during flowering time for their pollination services, while most wild bees cannot be moved to the crop but must be accommodated in the area near the crop. Honey bees produce honey, wax, and propolis, and wild bees are usually not exploited for nest products (except their offspring in the case of commercial mason bees).

Because of their morphology and behavior, honey bees are inefficient pollinators of some native plant crops in NNE, especially lowbush blueberry (Drummond 2016). Honey bees have short tongues — only about 6 mm long — which make it difficult for them from successfully reaching nectaries at the base of bell-like or tubular corollas of lowbush blueberry and many other native plants. Their flower handling behavior

can be ineffective (e.g., they do not buzz pollinate), their linear foraging pattern delimits their capacity for outcrossing pollen, and they will not forage in cold or rainy conditions (Drummond 2016).

Regardless of these shortcomings, honey bees are heavily relied upon by large-scale pollinator dependent agricultural systems in lowbush blueberry (ME), cranberry (MA), apple (all 4 states) and other crops in NNE. This is because honey bees can be concentrated at the crop during the bloom period, and are effective enough pollinators when stocking density is high (Asare et al. 2017). While honey bees belonging to local beekeepers contribute important crop pollination services in NNE, their numbers are low compared to rented hives brought from as far away as California. In 2016, ca. 83,000 honey bee colonies were trucked into ME in early May to pollinate the lowbush blueberry crop (A. Jadczak, Maine Department of Agriculture, personal communication), representing a gradual increase over the past five decades (Drummond 2012). The 83,000 hives brought to Maine in 2016 is 42 times greater than the number brought into the state for lowbush blueberry pollination in 1950 (Morse and Calderone 2000). Rented honey bees are stressed by their nomadic lifestyle, which includes a limited diet of flowers from a single plant species when they are on a crop. While wild bees are present in and around the lowbush blueberry fields, the risk of profit loss associated with reliance on wild bees alone is considered too great by many growers (Hanes et al. 2013, Asare et al. 2017). The relative contribution to fruit set by honey bees is 25.5%, and 38.7% by native bees. Year and cropping system contribute to the other 35.8% of the explained variance in fruit set. (Asare 2013, Yarborough et al. 2017); for other crops in NNE, we could not find estimates of proportions.

Decline of honey bees in NNE is part of a larger decline with implications for food security in North America and globally. As of about 1987, but first noted and named in 2006, a severe and ongoing decline in honey bees, including the failure of overwintering small apiaries and feral (unmanaged) colonies, was ascribed to Colony Collapse Disorder (CCD), a hive collapse phenomenon attributed especially to the Varroa mite (*Varroa destructor*). This ectoparasite is native to Asia (Wenner and Bushing 1996, Rosenkranz et al. 2010). It was inadvertently introduced in the U.S., and has since become ubiquitous in NNE and throughout the continental U.S. By 2006 the public had become aware that honey bees are in trouble. Most scientists agree that CCD stems from a multitude of stressors that include novel pathogens, intensive management practices, and pesticide exposure (Ellis et al. 2010, Neumann and Carreck 2010, Ratnieks and Carreck 2010, Drummond et al. 2012).

The loss of feral honey bee colonies exerts a compounding effect upon honey bee health in NNE and elsewhere, and is an ongoing concern. Such colonies in NNE were once resident, but not quantified, in hollow trees. These populations represented a pool of genetic variability in honey bees that helped to offset a depauperate genome after three genetic bottleneck events (upon introduction of honey bees to the New World, in response to introduction of parasitic mites, and upon consolidation of bee breeders). The loss of genetic diversity was exacerbated by the narrowly focused management of queen production in the U.S., and other factors (Cobey et al. 2011). Other factors that contribute to decline of feral honey bee colonies include a host of pathogens (bacteria, protozoans, fungi and viruses), arthropods such as tracheal mites, and indirect arthropod pests such as wax moths (Graham et al. 1992). Long, cold winters can also result in colony loss due to starvation (Morse 1990). The Maine Pollinator Protection Plan suggests that honey bees will continue to be available (Whitcomb and Additon 2015), but as of winter 2015-2016 the prognosis for honey bee overwintering in NNE was poor, with 44% loss across the U.S. (https://beeinformed.org/2016/05/10/nations-beekeepers-lost-44-percent-of-bees-in-2015-16/).

Overwintering survival of honey bee colonies continues to be low in NNE, probably due to pest and disease problems. In ME over the past decade honey bee colony losses over winter averaged from 40-50% (F.A. Drummond, personal communication). Survey results reported by Bee Informed (https://beeinformed.org/) suggest lower national loss rates over the past decade, averaging 28%. The difference between these percentages might be that ME estimates are derived mostly from small-scale hobby beekeepers, whereas the Bee Informed estimates are derived from both hobbyist and large-scale commercial beekeepers.

Honey bees are not the only introduced crop pollinators in NNE. Commercial bumble bees are typically added to lowbush blueberry fields at the rate of three to four colonies ("quads") per acre or about twice that per ha (Drummond 2012, Stubbs et al. 2001, Stubbs

and Drummond 2001). There are about 50-200 eastern bumble bee (*Bombus impatiens*) workers per colony depending upon the commercial supplier. Perhaps not all are closely related to the queen but put together from various colonies at the supplier's facility. Tongue length is about 5-15 mm. Foraging queens and their offspring fly in colder temperatures than honey bees, i.e., below 7.2°C, light mist, and wind (Drummond 2016), and have been seen foraging pre-sunrise and post-sunset. They perform buzz pollination, which is effective for movement of the sticky pollen of the lowbush blueberry flower. Their flight across the field is a non-directional zig-zag pattern that enhances outcrossing (Drummond 2016). A recent study in MA cranberry (Suni et al. 2017), where commercial bumble bee quads have also been deployed, showed that there were significant genetic differences among foraging *B. impatiens* and commercial quads. The data suggest that there was no widespread introgression of alleles from commercial bumble bees to wild bumble bees, and that commercial bumble bees did not become established in natural areas.

Additional species of native bees have been used to pollinate crops. For example, mason bees (*Osmia* spp.) in the family Megachilidae have been tried as managed pollinators for apple and lowbush blueberry in NNE. Diverse wild bees, including some in the genus *Osmia,* have been documented to be important pollinators for the lowbush blueberry crop (Blitzer et al. 2016, data from New York), and are somewhat common in NNE. Leaf cutter and mason bees appear to be nest-limited (Stubbs et al. 1997a). They can be trap nested or purchased. Trap nest dimensions for *Osmia atriventris* and many other native *Osmia* species associated with the ME lowbush blueberry agroecosystem are described in Stubbs et al. (2000). The species most available commercially is *Osmia lignaria*, the blue orchard bee; an order from a supplier can include about 250 females per unit, shipped in artificial nests of reeds or straws. Management requires phasing out nesting materials to reduce pathogenicity, with standardized approaches to release rates, handling, over-wintering, and other aspects. *Osmia* management is not trouble free, as there is potential that diseases and pests could spread across a continent. A Japanese bee, *Osmia corniforns*, which is accompanied by fungi from Japan, is expanding adventive populations in North America. The fungi affect native populations in the eastern U.S. of *Osmia lignaria* (Hedtke et al. 2015).

Another commercially available crop pollinator is the leafcutter bee, *Megachile*, also in the Megachilidae. A delivery of the European alfalfa leafcutter bee (*Megachile rotundata*) can have about 20,000 bees per order. These bees are used widely in the Pacific Northwest and Canada for pollinating the alfalfa seed crop. They have susceptibility to chalkbrood fungus, but otherwise their life history and cycle are similar to that of *Osmia lignaria*. These bees are active at ≥17.8°C, and are distinctive in that they partition each cell within the nest using pieces cut from flower petals, with about 15 petal cuttings per cell. Provisioning each egg involves about 15-30 bouts (trips) per cell to obtain pollen and nectar. Each tunnel has about 8-12 cells per tunnel. A female bee can produce 30-50 eggs, and can provision 2-4 tunnels in her lifetime. The tunnel size is 76-150 mm deep and 6-6.4 mm wide. Because these are multivoltine bees (with several generations per growing season), the manager must observe closely and phase out those nests that are unlikely to be productive. Field shelters are similar to those described above for mason bees, and the bees can over-winter as loose cells (Stubbs et al. 1997b). The alfalfa leafcutter bee can be used successfully to commercially pollinate lowbush blueberry (Stubbs and Drummond 1997). This bee was not adopted by commercial blueberry growers in ME because it requires incubation, emergence must be timed to coincide with flowering of the crop, and its foraging is poor during cool spring weather (Stubbs et al. 1997b).

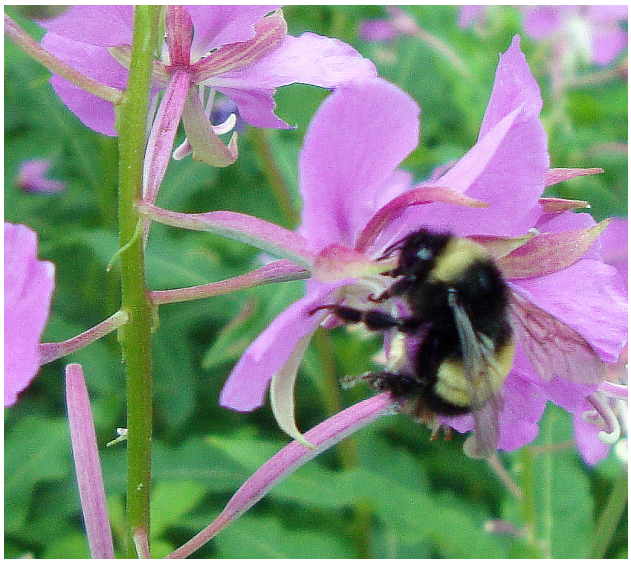
Wild bees may be stressed by competition at flowers from managed bees (e.g., honey bees, see Thomson 2004) and adventive bees, but this has not been shown for NNE (at least for lowbush blueberry in ME, Asare et al. 2017). Wild bees contract diseases or pick up pests on flowers also visited by honey bees (A.L. Averill unpublished data) and by managed eastern bumble bees (Bushmann et al. 2012), but here again, reports for NNE are few. Adventive bees have their own potential issues; for example, the wool-carder bee (*Anthidium manicatum*), which is spreading in NNE, is aggressive toward bumble bees at flowers of some garden plants (Gibbs and Sheffield 2009). Impacts of the giant resin bee and other adventive bees are unknown.

Nest sites for wild bees in NNE, a limiting factor?

Bee nests in NNE are cryptic, subtle, and typically integrated with floral resources; the sociality of the bee

(a)

(b)



(c)

(d)

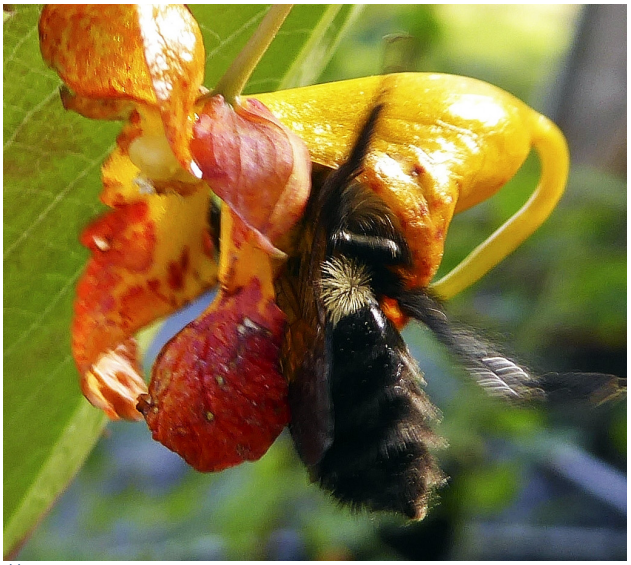
(e)

(f)

(g)

(h)

(i)



(j)

Figure 1. Bees of northern New England. (a) Bombus terricola *on white form of* Asclepias syriaca*, Blue Hill, ME, July 12, 2014; (b)* Bombus ternarius *queen on* Erica tetralix*, Brooklin, ME, April 23, 2014; (c)* Bombus terricola *on* Chaemerion angustifolium *at Mizpah Hut, Mt. Pierce, White Mountain National Forest, NH, elev. 1158 m, Aug 15, 2012; (d) wool carder bee,* Anthidium manicatum*, Blue Hill, ME, Sept 19, 2012; (e)* Andrena sp. *on* Salix sp.*, Brooklin, ME April 21, 2014, (f)* Ceratina dupla *on* Prunus*, Hampden, ME, June 23, 2014; (g)* Augochlora pura*, on* Gaillardia sp.*, Blue Hill, ME, Sept 21, 2015; (h)* Megachile sp.*, on* Lotus corniculatus*, Crampton, NH, Aug 18, 2013; (i)* Bombus impatiens *emerging from a commercial quad, Orono, ME, Sep 30, 2016 (Megan Leach photo); (j)* Bombus impatiens *visiting a flower of* Impatiens capensis *(Megan Leach photo). (Photos by A. C. Dibble unless attributed otherwise.)*

species of interest has considerable effect on the nest substrate and site. Bees in the Andrenidae, Colletidae, Megachilidae, and Melittidae have both solitary and communal nesting species while Apidae and Halictidae have solitary, communal, and social species (USDA-NRCS 2009). Social bees (eusocial) are characterized by cooperative brood care, with overlapping generations and division of labor. For solitary and communal bees, females construct individual (or in some cases, connecting communal) underground nests, provide food to offspring without aid from other bees, and often expire before brood emerges.

The majority of wild bee species of NNE nest in well-drained loamy soil in tunnels excavated by the females; sites include bare patches in roadside banks, lawns, lowbush blueberry fields, exposed soils at tip-up mounds, and woodland paths. In ME, ground-nesting bees tend to associate with sparse vegetation and a relatively shallow organic horizon (Osgood 1972). An aggregate nest of *Andrena crataegi* associated with a ME lowbush blueberry field was found to have interconnecting nest passages below ground but a shared burrow entrance (Osgood 1989). An example of a nest entrance for *Colletes compactus compactus* is shown in Figure 2a, with the nest occupied by both the host and its kleptoparasite (nest parasite, in which the parasite lays an egg in the nest of another bee species, without the original mother detecting the imposter egg), *Epeolus scutellaris*.

In NNE, nest sites can also include stone cavities, clay soils, pure fine sand (e.g., a nest of *Andrena carolina* in a child's sandbox in ME), pithy stems, and wood. Pithy stems such as in staghorn sumac (*Rhus typhina*), elderberry (*Sambucus* spp.), raspberry (*Rubus idaeus* ssp. *strigosus*), and blackberry (*Rubus* spp., especially *R. alleghaniensis*) are sometimes used as nests by *Ceratina* (Figure 1f), *Augochlora, Augochlorella, Lasioglossum*, and others. Branches browsed by deer or otherwise compromised may be used preferentially. Our anecdotal observations suggest there are nest opportunities between cedar shingles on buildings. Regarding nests in wood, galleries made by boring insects can later be occupied by leaf cutter bees (e.g., Megachilidae nests in borer holes in a sugar maple), while large carpenter bees (*Xylocopa virginiana*) excavate their own tunnels in wood.

Bumble bees build underground nests, for the most part. These bees are eusocial in that the queen lays eggs but depends on cooperation from her offspring to raise subsequent colony members (further details in Wilson 1971). In NNE bumble bees often occupy burrows abandoned by mice or chipmunks. Bumble bees can also nest in arboreal and surface level nests within naturally occurring substrates such as trees, rock crevices, or man-made structures (Goulson 2010), including an old mattress, bird house or insulation within a wall.

Limitation of nest sites could have consequences for wild bees in NNE. A study conducted over a four-year period in ME suggests that *Osmia* spp. bees are nest limited in boreal forest habitats (Stubbs et al. 1997a). Providing nests along the edge of blueberry fields increased *Osmia* populations foraging in the crop. However, a two-year study (F.A. Drummond unpublished data) in ME showed that artificial nests for bumble bees were rarely colonized (1 nest occupied in 2 years, 600 nests deployed), suggesting that bumble bees may not be nest limited in ME lowbush blueberry landscapes, or that the artificial nests were not recognized by the bees as suitable. Venturini et al. (2017c) showed that burned lowbush blueberry fields favored nesting of *Andrena spp.,* in that nest densities were significantly higher than in mowed fields. As pruning in lowbush blueberry fields shifts to mowing over burning due to cost and environmental concerns, nest sites for sand bees (Andrenidae) may become limiting in this agroecosystem.

Data to support usefulness of artificial nests can be contradictory. Such nests are intended to increase bee abundance near a crop or garden, and their installation is recommended as a conservation activity to enhance wild bees, but a positive outcome is not assured. Xerces, NRCS, and Sustainable Agriculture Research and Education (SARE) offer guidance concerning nest boxes. A design for block nests to support *Osmia* and *Megachile* is available (see Stubbs et al. 2000). In Ontario, Canada, MacIvor and Packer (2015) found in a three-year study of nesting boxes that introduced species of bees and wasps were more abundant than wild bees, and subject to lower parasitism rates. In ME, a four-year study deploying nest blocks increased wild native *Osmia* spp. densities in blueberry fields (Stubbs et al. 1997a). Also in ME, a five-year study resulted in findings of increased incidence of fungal pathogens (*Ascosphaera* spp.) and parasitic wasps in artificial nest sites (Drummond and Stubbs 1997). Whether this occurs in natural nests is not known. A non-replicated

observation of *Osmia* bees using artificial nest blocks attached to the side of a house in ME over a 21-year period has shown that while *Osmia* spp. communities fluctuate from year to year, the bees do persist over time (Drummond, personal observation). Bee hotels at the New England Wildflower Society's Garden in the Woods, Framingham, MA, and at University of New Hampshire, Durham, NH (S. Rehan, personal communication) inspire the public. However, sometimes wasps occupy the nests and there is no guarantee that bees will take up residence. A test of artificial ground nests 1 m square and 25 cm deep was conducted from 2013-2015 at four ME sites with 1400 one-min observations but resulted in negligible recorded bee activity (A.C. Dibble, unpublished data). The duration of that effort could be insufficient to gauge whether the technique is worthy of further exploration, but artificial soil nests for the alkali bee, *Nomia melanderi*, were successfully developed in the western U.S. to enhance alfalfa pollination (Cane 2008), so further attempts in NNE might be warranted.

Associated species

Some of the species that associate closely with bees, such as cuckoo bees (social parasites in the case of *Bombus* subgenus *Psithyrus*) or kleptoparasites, are thought to be more or less benign in that their populations are low enough not to cause loss of the host bee species. Many other associated species probably have a detrimental effect, especially if they are not native to eastern North America.

Parasitic bees and their vulnerability

About 20-25% of the bee community in NNE consists of bees that are nest parasites upon other species of native wild bees. Often, there is only one or a few host species (Bushmann 2013, Fowler 2016, Dibble et al. 2017). Parasitic bees can be divided into two kinds, the kleptoparasites, which with their hosts are all solitary bee species, and the social parasites in the case of Bombus subgenus Psithyrus. Both kinds do not build their own nests but have evolved instead as nest parasites dependent on other bee species. Parasitic bees often possess a minimum of body hairs and do not have structures for carrying pollen, though males and females can be found on flowers feeding on nectar. The extent of impact by both kinds upon their host species is unknown, but it appears possible that the parasitic bee species is vulnerable to decline of its host. Adverse conditions that affect the host, such as disease, flooding of the nest, or drought leading to scarce foraging resources could impact the parasitic species also.

The two kinds of parasitic bees can be separated by their biology. Regarding kleptoparasites, both host and parasitic bee species are solitary bees and the adults of both species are active during the same period each year. While the host female, who is at work provisioning her brood, is away from her nest the kleptoparasite female enters, lays her egg upon a pollen loaf prepared by the host, and departs (Mitchell 1960). An example from NNE of a host-kleptoparasite relationship is shown in Figure 2a-c, in which *Colletes compactus compactus* shares a nest with parasitic *Epeoloides scutellaris* in coastal ME. These two bee species are active in late August into mid-September when goldenrods are flowering (e.g., *Solidago rugosa, S. bicolor, S. puberula*). Following a drought during the late summer of 2016, in 2017 only a few male kleptoparasite individuals emerged from a documented population and none of the host species were found (A. C. Dibble, personal observation).

In the case of social parasites, the host bumble bee queen begins building up her colony in the spring. A parasitic queen (also a bumble bee, in subgenus *Psithyrus*) might enter the nest, kill the host queen, subjugate the host daughters, take over all egg-laying, and force the host colony to rear the parasite's brood. As an example of linked fates, Ashton's cuckoo bumble bee (*Bombus ashtoni*) is parasitic on the rusty patched bumble bee (*B. affinis*), and at least one other bumble bee species. It is found in NNE less often since the decline of *B. affinis*.

A total of nine bee genera from three families found in NNE contain parasitic species. In the family Apidae are Bombus (including the subgenus *Psithyrus*), *Epeoloides, Epeolus, Holcopasites, Triepeolus*, and *Nomada*; in the Halictidae is *Sphecodes*; and in the Megachilidae are Coelioxys and Stelis (USDA-NRCS 2009). Of these, Bombus, Epeoloides, Holcopasites, Stelis, Nomada, and Sphecodes contain species that are considered to be uncommon or rare in NNE, or their taxonomy remains incompletely resolved and not enough is known of their populations to assess their status. (Numerous other bee species in NNE may be rare but are not parasitic so their biology is not dependent on a host bee species.) Xerces lists *Epeoloides pusila* as "critically imperiled" in MA, but few parasitic bees in NNE are well-studied and more documentation is needed.

(a)

(b)

(c)

Pests and Pathogens

Numerous native and introduced species of microbes (beneficial and pathogenic), micro-parasites, and parasitoids are closely associated with bees in NNE. Some of these are relatively benign but others are debilitating and present a distinct threat to bees. We cover these briefly here to provide the scope of complexity involved in protection of bee diversity in NNE. We do not cover predators of bees in this review. Predators are diverse and comprise both vertebrate and invertebrate species in NNE. A good source for investigating bee predators is the Bumblebee Conservation Trust (https://bumblebeeconservation.org/about-bees/faqs/bumblebee-predators/).

Micro-parasites or disease causing pathogens

Disease is usually associated with density dependence resulting in periodic fluctuations in the host (Nokes 1992), in our case, the bee community. This may arise through shared use of flowers (Graystock et al. 2013). Local extinction of the host due to extremely virulent pathogens was suggested by Colla et al. (2006) to explain loss of some bumble bees that were formerly found in NNE. They suggest that a European strain or race of *Nosema bombi* (a native microsporidian pathogen) that arrived in North America with commercial bumble bees (*Bombus impatiens*) could have impacted vulnerable bee species. Bushmann et al. (2012) did not find evidence to support this hypothesis in ME lowbush blueberry production areas, and their findings were further supported by Cameron et al. (2016) who identified the North American strain as prevalent in declining *Bombus* on this continent. In ME infection rates of native *N. bombi* range from 1->50%, depending upon the bumble bee host species (Bushmann et al. 2012). The widespread *N. bombi* was present in North America before the commercial *Bombus* trade, so most

Figure 2. A native bee and its kleptoparasite. (a) Entrance to shared ground nest of two native solitary bees, host Colletes compactus compactus *and an associated kleptoparasite,* Epeolus scutellaris. *Hole is in center of photo, diameter about 8 mm; (b)* Colletes compactus compactus *mating at nest entrance, Brooklin, ME, Sept 14, 2015. Female bears a load of goldenrod pollen; (c) kleptoparasite* Epeolus scutellaris *female resting near nest entrance of its host* Colletes compactus compactus, *Brooklin, ME, Aug 27, 2016. (Photos by A. C. Dibble).*

likely this was not the more virulent, introduced strain. In all, pathogen "spillover", the movement of pathogens or parasites from commercially managed bees to wild bees (Colla et al. 2006), remains worrisome. Commercial bumble bee sources are making advances in assuring that pathogen spillover will not occur (Huang et al. 2016). Pathogen spillover from the introduced honey bee to populations of wild bees is also a high concern. In NNE, RNA viruses have recently been shown to be transmitted to wild bumble bees (Samantha Alger and Alex Burnham, University of Vermont, unpublished data). Several studies from Europe provide evidence that wild bee species are exposed to honey bee viruses (Graystock et al. 2013, Fürst et al. 2014, Ravoet et al. 2014), though the rate of infection remains under intensive research (Genersch et al. 2006, Fürst et al. 2014). Whether infection affects population dynamics of wild bees is unknown. Pathogens associated with wild bees are present at some background rate (Batra et al. 1973, MacFarlane et al. 1995) so any stresses on these populations may increase mortality in wild bee populations (Cariveau et al. 2014).

Macro-parasites

Macro-parasites of bees are primarily represented by members of the Arthropoda (Hexapoda: Diptera, Acari: Podapolipidae, Tarsnomidae, Varroidae), and the Nematoda (Mermithidae). Particularly troublesome among these are several species of hemolymph feeding honey bee parasitic mites (*Varroa destructor, Varroa jacobsoni,* and *Varroa* spp. yet to be described), which are recent parasites of honey bees (de Guzman and Rinderer 1999). They are thought to have moved to the European honey bee host from their original evolutionary host, *Apis cerana* (Anderson and Trueman 2000). This complex of parasitic mites is highly virulent to the European honey bee and facilitates transmission of several viruses (Rosenkranz et al. 2010, Tentcheva et al. 2004), including deformed wing virus (Wilfert et al. 2016). Fortunately, *Varroa* spp. do not appear to be capable of parasitizing and surviving upon bee hosts other than the honey bee (Potts et al. 2010). This host restriction may protect North American wild bee fauna.

Other parasitic mites common in North American bumble bees are the "tracheal mites," i.e., *Locustacaus buchneri* (Otterstatter and Whidden 2004). This native species has the potential to decimate colonies, though it tends to be much less virulent on bumble bees than *Varroa* mite is on honey bees (Otterstatter et al. 2005). There are many species of phoretic and predatory mites that infest wild bee species in North America (Eickwort 1994), but little is known of their biology and their impacts.

Conopidae: Many fly species in the family Conopidae (the Conopid flies or thick-headed flies) attack bumble bees and other bees. Some conopids are native to NNE. Adult conopid flies emerge in June in NNE to mate and then the female preys upon foraging hymenopterans at floral resources. She inserts a single egg through the intersegmental membrane of the host and into the abdomen (Pouvreau 1974, Schmid-Hempel et al. 1990, Müller et al. 1996, Goulson 2010). The egg hatches and the fly larva consumes hemolymph and gut tissue of the host, ultimately completely filling the abdomen and pupating to overwinter inside the host. Conopid fly parasitism alters bee behavior, including by inducing the host to dig its own 'grave' before its death, which is thought to enhance the probability of the parasitoid surviving the winter (Schmid-Hempel and Schmid-Hempel 1996, Schmid-Hempel et al. 1990, Malfi et al. 2014). Although the worker bumble bee still forages, the growing larva restricts the amount of nectar that can be contained in the honey stomach (Schmid-Hempel and Schmid-Hempel 1990, Goulson 2010). Because infected bumble bees live for a shorter period of time, it is possible that heavy conopid infestations can result in lowered colony growth and the reduced reproductive success of a colony (Schmid-Hempel and Schmid-Hempel 1988, Schmid-Hempel et al. 1990). Also, heavy infestation of a colony could result in rearing smaller queens, which can lower chances of queen survival through the winter (Müller and Schmid-Hempel 1992a, 1992b). In ME, Bickerman-Martens and F. A. Drummond (unpublished data) found 12-15% parasitism in 2012, 2014, and 2015 in 330 *Bombus* specimens but this varied by collection date. One day in mid-August 2015, >40% of all collected specimens had conopid larvae. A similar pattern was found in VT where 0-17% conopid attack was found in bumble bees, which varied by species and date of collection (L. L. Richardson unpublished data). In MA, Gillespie (2010) found 0-73% parasitism, depending on the day. Peaks in conopid prevalence likely coincide with the timing of the emergence of the adult flies from the previous year. Bickerman-Martens and Drummond (2015) found that region was the only significant variable for predicting

conopid parasitism rates. Similarly, in Switzerland, Schmid-Hempel et al. (1990) found that study area was one of the most important factors in predicting parasitism. No significant correlation could be found between parasitism rates and (1) *Bombus* abundance in MA (Gillespie and Adler 2013), or (2) plant species on which the host was foraging in Alberta, Canada (Otterstatter 2001).

Nematodes: Nematode parasites are common in North American bumble bee fauna (Kaya 1987). Mermithid nematodes are parasites that usually kill the host bumble bee worker or queen, but their incidence tends to be low in natural populations (Schmid-Hempel 1998). We have found them parasitizing bumble bees in ME at levels of <1.0% (Bickerman-Martens and Drummond, unpublished data). *Sphaerularia bombi* is a nematode parasite that infects bumblebee queens. In most cases, infected queens do not sufficiently develop their ovaries to establish nests (Ponoir and van der Lann 1972; MacFarlane et al. 1995). In a recent survey of 217 *Bombus* queens in southeastern MA, 3.7% were infected with *S. bombi* (A. L. Averill, unpublished). In general, nematodes have not been well studied and there is little information, except on bumble bee hosts, regarding their significance to the health of bee fauna in North America.

RELATIONSHIPS BETWEEN BEES AND PLANTS

For many of the bees and the >3,000 native plants in NNE (NatureServe 2016), the host plant relationships and plant reproductive requirements are incompletely known. McCall and Primack (1992), and Primack and Inouye (1993) profiled pollination systems in a lowland forest west of Boston, MA and alpine habitat in NH, but most habitats in NNE are not similarly analyzed for pollinator resources. The majority of NNE plants are thought to be not wholly dependent on any one or a few bee species. In NNE bee gardens, plant selection that favors the specialists will likely meet needs of generalist bees also (Fowler 2016). The proportion of the flora visited by bees has not been quantified. For discrete areas, the proportion of bee-visited plants can be estimated somewhat crudely but this requires assumptions based on related plant species. A flora for the 1,618-ha Penobscot Experimental Forest (Dibble 2013) documented 344 plant species, of which 61 species are not native and 10 are invasive. About 200 plant species, or 58% of the total, were estimated as likely to be visited by insects, especially bees. Dibble et al. (1999) found that presence of insect-visited native understory plants of red spruce (*Picea rubens*) forests in central and northern ME is one of the indicators of regeneration habitat that favors red spruce.

Bee communities have been documented in NNE based on their association with plant species or groups in the native NNE flora. Among many examples are bees that visit the heath family (Ericaceae), which have received considerable research attention, including black huckleberry (*Gaylussacia baccata*) (Lovell 1940), lowbush blueberry (*Vaccinium angustifolium*) (Stubbs et al. 1992, Bushmann 2013, Bushmann and Drummond 2015, F.A. Drummond et al., in press), and cranberry (*Vaccinium macrocarpon*) (MacKenzie and Averill 1995, Loose et al. 2005, Averill et al., in press). Bee communities associated with two floral morphologies in shadbush (*Amelanchier*) were studied by Dibble and Drummond (1997) and Dibble et al. (1997), who found pollen-bearing petals (andropetaly) in Nantucket shadbush (*A. nantucketensis*), and among more than 40 bee species a small guild (subset) associated with tiny, pollen-bearing petals but not large petals. Some other examples in which pollinator communities were documented include swamp loosestrife (*Decodon verticillatus*) (Eckert 2002), and two species of aster (*Symphyotrichum lanceolatum* and *S. lateriflorum*), Horsburgh et al. (2011).

Dependence upon animal pollinators varies from independence (pollination by wind, water, or by automatic selfing) to complete dependence. A prominent example of a native wild crop plant that requires an insect for effective pollination is lowbush blueberry (Bell et al. 2009). Many orchids in NNE require insects for pollination, including especially the pink lady's slipper (*Cypripedium acaule*), which depends upon the visit of a *Bombus* queen — the only member of the colony active in late May-June when these plants flower (Plowright et al. 1980, Argue 2011); the insect effects removal of pollinia, or masses of pollen, from one flower and delivers them to the flower of another plant. In the orchid genus *Spiranthes* of eastern North America, most species are pollinated by long-tongued bees (some species of *Bombus*, Megachilids) while *S. lucida* is pollinated by Halictine (short-tongued) bees (Catling 1983). VT populations of turtlehead (*Chelone glabra*) are most effectively pollinated by *Bombus vagans* while other

insect visitors have negligible roles (Richardson and Irwin 2015). Floral rewards are only part of the picture, and turtlehead exemplifies plants that have secondary metabolites that bees might use to self-medicate. In a field experiment, bumble bees that bore protozoan parasites (*Crithidia bombi*, a gut parasite of bumble bees) stayed longer on and returned more often to flowers treated with higher concentrations of iridoid glycosides in their nectar than they did on flowers treated with low concentrations (Richardson et al. 2016).

Among native plants of NNE that rely at least partially for their pollination upon bees are some common plants that also provide excellent forage for wild bees. Dioecious plants such as willow (*Salix* spp.) and hollies (*Ilex* spp.) presumably require insects (and to some extent perhaps wind) to move pollen between staminate and carpellate individuals. Three cherry species, pin cherry (*Prunus pensylvanica*), black cherry (*P. serotina*), and choke cherry (*P. virginiana*), are at least partially insect-pollinated (Shiell et al. 2002). Degree of reliance on insect pollinators is not fully known in shadbush (*Amelanchier*), though species have been shown to vary in percent of facultative apomixis, or asexual seed production (Campbell et al. 1987).

In forests, bees differ in their abundance and species diversity according to light conditions and other factors. Bees are expected to be infrequent in shady conifer-dominated forests because of relative lack of flowers, though the bee community can be diverse in conifer forest openings (Miliczky and Osgood 1979a, 1979b). Some hardwood forests in western MA have readily observable bee communities that increase in abundance and species diversity with gap size and are associated with lower-growing vegetation, while a few bee guilds do not follow the general pattern (Roberts et al. 2018). When understory light conditions increase due to logging or other disturbance, then the bee community is likely to increase in abundance and diversity. Romey et al. 2007 found an increase in bee abundance associated with goldenrod (*Solidago* spp.) and brambles (*Rubus* spp.) after logging in a hardwood forest in New York. In closed canopies, bees are presumably present though at low density and could be necessary for pollination of some understory plants. Boufford (1987) found that a shade-adapted understory herb, enchanter's nightshade (*Circaea* sp.), is pollinated by Halictidae and Syrphid flies. A shade-adapted shrub, witch-hazel (*Hamamelis virginiana*), attracts Halictidae and many kinds of insects despite its flowering season of late September into December in Connecticut (Anderson and Hill 2002); this species can flower into late autumn in northern ME. Shade tolerant forest herbs common in NNE that are visited by bees include Canada mayflower (*Maianthemum canadense*), painted trillium (*Trillium undulatum*), side-bells wintergreen (*Orthilia secunda*), bunchberry (*Chamaepericlymenum canadensis*), and others investigated by Barrett and Helenurm (1987). Some herbs of deciduous forests are spring ephemerals that flower before tree leaf expansion, and early bees in forests visit their flowers, e.g., bluebead lily (*Clintonia borealis*), trout lily (*Erythronium albidum*), and sessile-leaf bellwort (*Uvularia sessilifolia*).

Native versus non-native herbaceous plants as resources for bees

There has been much interest in whether the origin of a plant species (native versus non-native) makes a difference to bees. Several studies from other regions of the U.S. suggest that wild bees tend to favor native plants (Corbet et al. 2001, Morales and Traveset 2009, Morandin and Kremin 2013, Harmon-Threatt and Kremen 2015, Salisbury et al. 2015), though numerous non-native species are also frequently visited by bees (Hanley et al. 2014, Salisbury et al. 2015). In ME, wild bees (not including bumble bees) were more abundant on a diverse mix of mostly native wildflowers, while honey bees and bumble bees were more abundant on non-native clovers, especially yellow sweet clover (*Melilotus officinalis*) (Venturini et al. 2017b). Heinrich (1979) concluded that selection by bees is probably based on abundance, floral display, sugar content of nectar, etc. rather than on status as native versus introduced in North America.

Bees might favor native plants of unimproved local genotypes over some improved cultivars. Plants selected for traits that people prefer, even among plant species considered 'native', can attract fewer pollinators than their wildtype counterparts (White 2016). With growing demand for native plants in NNE has come an interest in native cultivars or "nativars." These may be sold in garden centers and plant catalogs as "native," but have not grown naturally in the wild. Nativars were selected for or developed and then maintained through propagation because they exhibit robust, predictable habits in domestic gardens, or they have desirable size, foliage color, flower qualities, extended flowering period, sterility, or disease resistance. Researchers in VT compared

Table 2. Selected plants that grow in northern New England and have potential in bee gardens, listed by their approximate flowering season, with pollinators they attract and comments. * = introduced and may fill a gap in the season when native vegetation offers relatively few flowers. T=tree, S=shrub, P=perennial, B=biennial, A=annual, D=tolerates dry site, M=requires moist soil, Sh=tolerates part shade, L=relatively long bloom period (> 1 month), !=may spread beyond intended area in garden, SS=self sows but is not overly aggressive.

Species name	Flowering season	Observed pollinators	Comments
Salix spp. (willow)	Very early	Andrenids, *Bombus* queens, other small bees	S; important early season food; native species are excellent; non-native *Salix chaenomeloides* (Japanese willow) is even earlier
**Crocus vernus* (crocus)	Very early	Andrenids	Spring bulb, obtain from pesticide-free source
**Taraxacum officinale* (dandelion)	Early spring	*Bombus*, Andrenids	B, !
Vaccinium angustifolium (lowbush blueberry)	Early spring	*Bombus*, Honey bee, Andrenids, small bees	S
Prunus spp. (cherry)	Mid-spring	Many kinds of bees	S, T; plant native species
Rhododendron canadense (rhodora)	Mid-spring	*Bombus*	S, M, Sh
Rubus spp. (brambles)	Late spring, early summer	Many kinds of bees	S, !
Zizia aurea (golden Alexander)	Late spring	Some specialist sweat bees	P, M
Angelica spp. (angelica)	Mid to late summer	Many kinds of bees	P; plant native species
Ceanothus americanus (New Jersey tea)	Late summer	Many kinds of bees	S, D
**Gaillardia aristata, G. pulchella* (blanketflower)	Summer into Fall	*Bombus*, Halictids	A
Impatiens capensis (jewelweed)	Summer into Fall	*Bombus*, hummingbirds	A, L,SS
Penstemon digitalis (beardtongue)	Mid-summer	*Bombus*	P; wild-type preferred
Dasiphora fruticosa (shrubby cinquefoil)	Summer into Fall	Honeybees, Halictids	D
Rhus typhina, R. glabra (sumac)	Early to mid-summer	Many kinds of bees	S, ! (a large shrub); used by stem-nesting bees also
Rosa spp. (rose)	Late spring into summer	*Bombus*, other bees	S, !; avoid invasive species (e.g., *Rosa multiflora*)
**Origanum vulgare* ssp. *hirtum* (Greek oregano)	Early summer into Fall	Honey bees, *Bombus*, small bees	P, L
Asclepias syriaca (common milkweed)	Mid-summer	Bees of all kinds, a host plant of monarch butterfly	P, !; visited by yellow banded bumble bee
Asclepias tuberosa (butterfly milkweed)	Mid-summer	*Bombus*, small bees, a host plant of monarch butterfly	P; not long-lived, plan to re-plant every 3-5 years
Spiraea alba var. *latifolia* (meadowsweet)	Mid-summer	Numerous kinds of bees and other insects	S, L, Sh
Tilia americana (American basswood)	Early summer	*Bombus*, honey bees, other bees	T
Liatris spicata, L. scariosa, L. novae-angliae (blazing star)	Mid-summer	*Bombus* and many other bees	P, D
Mentha spp. (mint)	Mid-summer	*Bombus* and many other bees	P, SS, !; plant native species
**Nepeta cataria* (catmint)	Mid-summer	*Bombus* and many other bees	P, L; cut back after flowering for a second flush of bloom

Table 2. Continued

Species name	Flowering season	Observed pollinators	Comments
Cephalanthus occidentalis (buttonbush)	Summer	Honey bees, some Megachilids	S, M, Sh
**Phacelia tanacetifolia* (bee's friend)	Summer into fall	*Bombus,* honey bees	A, SS, L, D
**Borago officinalis* (borage)	Summer into fall	Honey bee, *Bombus*, Halictids	A
Cirsium muticum (swamp thistle)	Mid-summer	*Bombus*, many small bees	P,M; a native species, tolerates a wet site
Parthenocissus quinquefolia (Virginia creeper)	Mid-July into August	Honey bees, *Bombus*, many small bees	Vine, !, Sh; fruits for wildlife
Clethra alnifolia (summersweet)	Mid-summer into Early fall	Honey bees, *Bombus*, many small bees	S, M, !, Sh
Helianthus annuus (wild sunflower)	Late summer	Honey bee, *Bombus*, *Melissodes*	A, D
Monarda fistulosa, M. media, others (bee balm)	Mid-summer into Sept	*Bombus*, many small bees, hummingbirds	P
Pycnanthemum, various spp. (mountain mint)	Mid-summer into Sept	*Bombus*, small bees	P, L
Eurybia macrophylla (big-leaf aster)	Late summer into fall	Many small bees	P, Sh
**Trifolium repens* (white clover)	Summer into fall	*Bombus,* honey bees, other bees	P; can be mowed in a lawn
**Trifolium pratense* (red clover)	Early and mid-summer	*Bombus,* other bees that have long tongues	P; not long lived; for a meadow planting
**Thymus vulgaris* (thyme)	Summer into fall	*Bombus* and other smaller bees	P; can be mowed in a lawn
Eutrochium maculatum (Joe pye-weed)	Late summer	*Bombus* and other bee spp., fritillary butterflies	P, M
**Calendula officinalis* (pot marigold)	Aug-Oct	*Bombus*, Halictids	A, SS; flowers until hard frost
Solidago puberula, S. bicolor, other spp. (goldenrod)	Aug-Oct	*Bombus*, *Colletes*, small bees	P, D
Symphyotrichum novae-angliae (New England aster)	Mid Sept-early Oct	*Bombus*, small bees	P
**Gentiana clausa, G. andrewsii, G. catesbaei* (gentian)	Late Sept-late Oct	*Bombus*	P

flower visitation by all insect pollinators on native herbaceous plant species versus those on a cultivar of the same species (study site shown in Figure 3a). Both honey bees and wild bees were more abundant on native species over cultivated varieties of the native species, but not always, and not exclusively (White 2016). Some native cultivars may be comparable substitutions for native species in pollinator habitat restoration projects, but each cultivar should be evaluated on an individual basis. In a VT study of purple coneflower (*Echinacea purpurea*) and three of its cultivars, double-flowered and hybridized cultivars were significantly less attractive to pollinators than the species (White 2016). Similarly, for enhancing bee habitat, growers can favor milkweeds, poppies, sages, mints, oregano, and numerous others mentioned in Table 2 over daffodils (*Narcissus* sp.), tulips (*Tulipa* spp.), daylilies (*Hemerocallis flava, H. fulva*, and cultivars), and heathers (*Calluna* spp.), which appear to receive few visits from bees in NNE.

Woody plants as resources for bees

Many native species of trees and shrubs of NNE have particular importance to bees because they offer an abundant floral resource, perhaps at a time when flowers otherwise are scarce. Willows (*Salix* spp.) and maples (*Acer* spp.) flower earlier than most plants in

NNE, coinciding with the active period for the earliest wild bees (Andrenids, *Bombus*) (Stubbs et al. 1992). Other examples are cherries and shadbush, mentioned above, plus American basswood (*Tilia americana*). Pollen from some wind-pollinated trees and shrubs, including the oaks (*Quercus* spp.) may be used by bees (Stubbs et al. 1992, MacIvor et al. 2014). In ME we have observed rented honey bees collecting pollen from speckled alder (*Alnus incana* ssp. *rubra*) just prior to the lowbush blueberry bloom period. Smaller trees or large shrubs of the region are also visited by bees, including those mentioned above plus dogwoods (*Swida* or *Cornus* spp.) and hawthorn (*Crataegus* spp.). Many more shrubs of low to medium height provide forage for bees including summersweet, a.k.a. coastal sweet pepperbush (*Clethra alnifolia*), meadowsweet (*Spiraea alba* var. *latifolia*), New Jersey tea (*Ceanothus americana*), viburnum (*Viburnum acerifolium, V. lantanoides, V. recognitum*, *V. lentago*, *V. nudum* ssp. *cassinoides,* and others), holly (*Ilex mucronata, I. glabra,* and *I. verticillata*), northern shrub honeysuckle (*Lonicera canadensis*), huckleberry (*Gaylussacia* spp.), blueberry (*Vaccinium* spp.), raspberry, blackberry (*Rubus* spp.), and cranberry (*Vaccinium macrocarpon*) (Table 2). Subshrubs visited by bees in forests include trailing arbutus (*Epigaea repens*), which is visited by *Bombus* queens in April, plus wild sarsaparilla (*Aralia nudicaulis*) and mountain cranberry (*Vaccinium vitis-idaea* var. *minus*).

BEE HABITATS

Habitat loss

Among the threats to pollinators are habitat fragmentation, degradation (e.g., change in land use, exposure to pesticides, frequent mowing, forest succession, invasive plants), or outright loss (e.g., a natural area is converted to pavement, roof, intensively managed lawn, or plowed field). Some of these factors could jeopardize bee populations, though direct evidence is lacking in NNE. With reduced habitat, extinctions of bees and their host plants becomes more likely.

Some bee species might be more vulnerable than others, especially those that specialize upon endemic (found nowhere else) plant species. Examples of bee-visited plant taxa endemic in New England are: Robbin's milk-vetch (*Astragalus robbinsii* var. *robbinsii*), Jesup's milk-vetch (*Astragalus robbinsii* var. *jesupii*), Bicknell's hawthorn (*Crataegus bicknellii*), Kennedy's hawthorn (*Crataegus kennedyi*), cleft-leaved hawthorn (*Crataegus schizophylla*), New England thoroughwort (*Eupatorium novae-angliae*), and Robbins' cinquefoil (*Potentilla robbinsiana*) (NEWFS 2015). It seems unlikely that any of these examples have species-specific relationships with their pollinators, but that has not been determined and needs study.

Later-season floral resources could be in short supply in NNE, and this represents a form of habitat loss. By early September, mowing at roadsides, on landfills, and elsewhere typically reduces the flower count many-fold; goldenrods and asters are among the native plants that become less available, and may be diminished to the point where they are unable to provide forage for late summer bees (especially some *Andrena* species, *Bombus*, *Colletes compactus*, *Hylaeus, Melissodes*, and numerous Halictidae including multivoltine species such as *Augochlorella aurata*). Repeated and intensive mowing in autumn could have particular consequences for *Bombus* species, as the new gynes are available for mating and need to increase fat reserves for their upcoming hibernation.

Forest succession and bee habitat

Distribution of bees within forest strata, and especially those associated with upper strata in a closed canopy, has not been much measured in NNE. The region shares some bee species that were found in upper strata in a study in Georgia, U.S.A. (Ulyshen et al. 2010), including *Augochlora pura* (Figure 1g), a common sweat bee. Bees that frequent the forest floor tend to receive greater attention because they are more readily observed, but canopy trees such as red maple, black tupelo (*Nyssa sylvatica* var. *sylvatica*), black cherry, and American basswood are visited by bees when in flower. American chestnut (*Castanea dentata*) was once a dominant tree in parts of NNE, and might have provided a pulse of pollen for bees, though we could find no data regarding this.

Remnant stone walls in contemporary forests of NNE are reminders that vast treeless areas, which were farm fields, once characterized much of the landscape, with views from horizon to horizon in many parts of the region. This represents a deforestation event that had undocumented effects on bee populations, but presumably bee habitats expanded greatly over closed canopy conditions from presettlement times.

Reforestation proceeded as of about the mid 1800s, by which time many farmers of NNE had abandoned thin, rocky soils in favor of deeper soils in the upper Midwest (Wessels 1997), and presumably bee habitats contracted as pastures and plowed fields grew back to closed canopy forest. This history can be considered as a context for recent findings that openings in the canopy are typically accompanied by expanded bee forage with early-successional plants, increased nest habitats, and greater bee abundance (pine woodlands in New Jersey, Winfree et al. 2007). An association between bee abundance and early-successional flora in forest openings was quantified for northwestern Ontario (Fye 1972), and that study features many plant species common in NNE. Herbs (e.g., fireweed, *Chaemerion angustifolium*), shrubs and small trees (raspberry, pin cherry, staghorn sumac, ericaceous shrubs) that are visited by bees can temporarily dominate an opening.

Open sky may benefit bees in that some bee species orient by a sun-compass (Dickinson 1994) along with landmarks. This could have consequences for host plants. O'Connell and Johnston (1998) found greater fruit set in pink lady's slipper, an orchid that requires the visit of a bumble bee, where there was more open sky above the plants. Some plants may be sensitive to the amount of open sky in their environment; pink lady's slipper rarely grows in open fields, and there are many other forest herbs and some shrubs that appear to require at least a partial canopy as they are seldom found in full sun of large openings.

Land use alterations and bee habitat

As forest succession proceeds, the gradual diminishing of habitats used by bees, due to shade and insufficient forage, may be offset by edges, roadsides, gaps, utility corridors, solar farms, and wind tower sites that continue to offer forage. Semi-natural or minimally managed vegetation might become aggregated into urban development with extensive paved areas and closely mowed lawns. Examples of intensive vegetation management are easily found, as roadsides are typically mowed or sprayed to keep vegetation down and maintain sight lines for motorists. Railroad corridors are heavily treated with herbicides because owners of the rail system are required by law to reduce vegetation that might ignite and cause wildfire. A widespread perception that a tidy lawn is preferable to a patch of diverse flowers still predominates in many parts of NNE.

These aspects often result in a tendency toward reduction in plant diversity with urbanization, as documented for Needham, MA by Standley (2003). The build-out of the coastal plain diminished native plant communities to remnants in many places, e.g., in the cranberry-growing areas of southeastern MA; bee diversity has also decreased there in recent years (A. L. Averill et al., in press). Bees of urban environments have been studied in or near New York City (Matteson et al. 2008, Fetridge et al. 2008, Matteson and Langelloto 2010), but not much in population centers of NNE; the lack of plant diversity could severely limit bee diversity in such environments.

Fifteen bee habitat types of NNE

We developed a list of 15 habitats (Table 3) that can be used as a framework for examining what is known about bee use of vegetation types, floral resources, and anthropogenic habitats in NNE. Seminatural habitats such as those studied by Williams and Kremen (2007) in California can be approximated among NNE habitats, though they are dominated by different plant species and attract bee species with few overlaps among those found in their study.

The first part of our list consists of types that are natural or at least dominated by native vegetation, such as closed canopy hardwood (Figure 3b) and conifer-dominated forests, recent clear cuts, wetlands, coastal dunes (Figure 3c), islands, shores, and alpine zones (Figure 3d). The second part consists of anthropogenic habitats such as farms (Fig. 3a), areas occupied by residences and businesses in varying concentrations (e.g., urban and suburban), transportation and utility corridors, and heavily disturbed areas such as closed landfills and reclaimed minelands. Several aspects are brought out by this exercise: (1) the importance of pesticide exposure because in any of these habitats, spray drift or exposure from a pesticide application could degrade habitat, at least temporarily; (2) in crop areas, a single monoculture over thousands of acres, such as in the ME lowbush blueberry barrens, can be limiting to bees if surrounding vegetation is managed intensively so that flowers other than the crop plants are lacking; (3) the extent of mowing along highways, at homes and businesses, and in parks, probably affects bee abundance and diversity for an area (Lerman and Milam 2016, Lerman et al. 2018). A study of bee diversity on ME coastal islands will be reported separately

(S.L. Bushmann unpublished data), and we have documented an unusual bee assemblage on a remote island in Washington Co., ME (A.C. Dibble unpublished data). The alpine zone, or any higher-elevation habitat above treeline, remains virtually unexplored in NNE for bee diversity, except efforts in a BioBlitz at White Mountain National Forest in June 2015 (Tucker and Rehan 2017).

Management of openings has much to do with bee abundance. Habitats that are not mowed intensively, such as pastures, meadows, fields, riparian areas, farms and gardens, prairies, dune systems, utility corridors, recently harvested forest, and forest gaps within mature stands, are more likely to have an abundance of bees compared to nearby mowed areas. This pattern was verified in the Downeast region of ME (Groff et al. 2016). Mowing of openings has the benefit of maintaining vegetation in early succession, but could be less useful to bees in the short term if flowers are repeatedly cut off. Some low-growing plants that offer flowers visited by bees, despite close mowing, include violets (*Viola* spp.), wild strawberry (*Fragaria virginiana*), creeping Charlie (*Glechoma hederacea*, a weed), clover species, and common thyme (*Thymus officinalis*). Hay fields may be overall relatively poor habitat if they are in active management for high quality grass-dominated hay, but management of hay fields can be compatible with goals for bee habitat (see below).

Additional anthropogenic and natural habitats in NNE are not yet well-quantified regarding their relative value as bee habitats. Among the former, perpetual openings such as corridors associated with roads, railroads and utilities, waste areas, landfill caps, lawns, and ball fields vary in their quality of habitat for bees, probably based on the intensity of mowing or other vegetation control, and on surrounding vegetation. Islands, montane areas and sandy soils might harbor unusual bee species or genetic variability but these habitats have not yet been well-documented for the most part (exception: Goldstein and Ascher 2016). These are among habitats identified by Dibble et al. (2017) as a priority for further sampling regarding bee diversity in ME.

Invasive plants — boon or bust for bees?

When flowers of invasive plants are present in abundance, this would seem to present an opportunity for generalist wild bees and honey bees. Invasive plants far exceed their intended plantings, or they arrived inadvertently and have rapidly spread to dominate large areas. Such plants can out-compete native plants (those historically indigenous prior to European colonization, according to the plants.usda.gov database, USDA-NRCS 2018) with which the wild bees evolved. While native plants offer a succession of flowers during the growing season, the resources are patchy, and a continuous succession of floral resources may not be available in some locations. Forage opportunities are reduced in diversity and length of time when a few invasive plant species occupy much of the habitat. Woods (1993) in MA and VT found that invasive Tatarian honeysuckle (*Lonicera tatarica*) has clear impacts on native plant diversity. McKinney and Goodell (2010) in Ohio examined impacts of invasive Amur honeysuckle (*Lonicera maackii*) upon native wild geranium (*Geranium maculatum*). These studies suggest that as such plants spread, bee forage opportunities upon native plants are lost, as are fruit and seed production in the native plant species. The native plants may have insufficient pollination to maintain populations (Menz et al. 2011). Evolutionary relationships between bees and their host plants might be disrupted. Examples of invasive plants in NNE are Japanese barberry (*Berberis thunbergii*) (Silander and Klepeis 1999), glossy buckthorn (*Frangula alnus*), common buckthorn (*Rhamnus cathartica*), black swallow-wort (*Cynanchum louiseae*), Oriental bittersweet (*Celastrus orbiculatus*), Himalayan balsam (*Impatiens glandulifera*), garden heliotrope or valerian (*Valeriana officinalis*), purple loosestrife (*Lythrum salicaria*), multiflora rose (*Rosa multiflora*), tall lupine (*Lupinus polyphyllus*), autumn olive (*Elaeagnus umbellata*), and Japanese knotweed (*Fallopia japonica*). Several invasive grasses impact bee habitats, and are apparently not much visited by bees. These include common reed (*Phragmites australis*) and reed canarygrass (*Phalaris arundinacea*), which can both rapidly fill ditches and moist meadows in NNE. To an unmeasured extent, they displace diverse species of native plants that attract bees.

Whether invasive plants improve or degrade bee habitat is not known in NNE. One aspect, the comparative nutrition of native vs. invasive plant resources, especially nectar and pollen, remains unquantified. Relative attractiveness of native vs. invasive plants was studied by Stubbs et al. (2008) in ME among three pairs of invasive and native plants that co-flower. Lowbush blueberry had lower fruit set if located near Japanese barberry, compared to lowbush blueberry distant from

the invasive plant. Detrimental reproductive effects were not found in native wild raisin (*Viburnum nudum*) growing near patches of invasive glossy buckthorn, or in native meadowsweet that grew near invasive purple loosestrife.

Beekeepers in NNE have a dilemma regarding invasive plants. They are reluctant to control Japanese knotweed because of its abundant late-season flowers and abundant nectar secretion, but this plant spreads into and dominates riparian habitats and can take over areas at field edges (for a history of its introduction and spread in North America, see Townsend 1997). Some beekeepers also resist controlling purple loosestrife with its abundant flowers in August, and want to retain June-flowering black locust (*Robinia pseudoacacia*), a tree native in Pennsylvania and farther south. In the case of black locust, habitat loss is due partly because the tree lacks flammability, and can change the fire regime in fire-adapted forest types such as those dominated by pitch pine (*Pinus rigida*; Dibble and Rees 2005). The consequence for wild bees is forest conversion from fire-adapted woodland vegetation that supports diverse herbs and shrubs on which they forage, to a shady mesic stand with little understory vegetation suitable as bee forage. Examples of pitch pine forest can be found in sandy outwash plains in all four states, less so in VT where the type is rare (Siccama 1971).

Other invasive plants in NNE differ from native species in their response to wildfire and fuel characteristics (Dibble et al. 2007, Dibble et al. 2008), with implications for retaining quality bee forage. In vegetation types that require periodic fire to maintain plant diversity, the forest might cease to burn readily, or at all. The shady understory is expected to have few bees compared to openings and woodland conditions (Winfree et al. 2007), yet many invasive shrubs and herb species are shade tolerant and can form a dense understory in NNE (Dibble and Rees 2005).

The best time to control invasive plant populations is when the plants are few and scattered. For the sake of bee habitat and many other conservation priorities, the propensity of invasive plants to dominate habitat makes them too risky to allow unchecked spread. Eradication may not be practical, but persistent control efforts will help keep them from overwhelming natural areas, fallow fields, and edge habitats that support wild bees and honey bees.

Crops as habitat

Much of the pollinator habitat literature in NNE focuses on bee habitat as relevant to agriculture (e.g., Loose et al. 2005, Stubbs et al. 1992, Drummond et al. 2017), and we know more about crop habitats than about most other kinds of habitats. A trend towards local, smaller, less intensive agriculture in NNE may increase habitat heterogeneity and reverse the negative impacts of agricultural intensification on pollinators (Deguines et al. 2014). Organic farms may support greater diversity of pollinators than conventional farms, at both the farm and landscape scale (Gabriel et al. 2010, Kremen and Miles 2012, although see Bushmann and Drummond 2015 in regards to lowbush blueberry). In NNE the number of organic farms has increased by 102.8% from 2000-2011, whereas the percentage of all (conventional and organic) farms (2002-2012) increased by only 19.2% (USDA-ERS 2016). Some additional aspects of crops as habitat are presented here.

Insecticides and other pesticides

In NNE, pests such as Colorado potato beetle, squash bug, codling moth, imported cabbage worm, tobacco hornworm, flea beetles, aphids, and numerous other common pests may make it extremely difficult to make a profit in farming. For pollinator dependent crops, major pests include apple maggot fly, plum curculio, striped cucumber beetle, tarnish plant bug, codling moth, blueberry maggot fly, spotted wing drosophila, and cranberry fruit worm.

To reduce costs and unintended harm to pollinators, an Integrated Pest Management Plan (IPM, Dent 1995, Philips et al. 2014) is highly recommended. This is a management framework that involves identifying the suspected pest, determining whether some threshold level of damage has been exceeded, and if necessary, then treating with the least toxic method (i.e., hand-picking pest insects into soapy water) or tactical application of the most pest-specific pesticide in the lowest effective dose that will reduce the pest presence back below the threshold. In addition, farmers practicing IPM are also encouraged to design their cropping system to best take advantage of natural biological controls. IPM improves habitat for beneficial insects, saves money and labor, cuts down on health risks to people, helps prevent buildup of resistance to pesticides in pest populations, and protects water quality. Where certain crops are impossible to grow without heavy application of pesticides,

Table 3. Selected bee habitats in northern New England, with representative examples. Relative abundance is roughly estimated. "Common"=readily found, abundant and widespread in all four states; "Local"=abundant in some places but not necessarily shared across all four states, "Infrequent"=not common but can be found; "Rare"=seldom-encountered and not well-studied regarding pollinator habitat.

Habitat type	Example	Estimated abundance	Further information	Comments
Closed canopy hardwood forest with small openings	Green Mountain National Forest, VT	Common	Giles and Ascher 2006	Expected to have relatively low diversity and abundance of bees
Closed canopy conifer-dominated forest with small openings	Penobscot Experimental Forest, Bradley, ME	Common	Dibble 2013; Groff et al. 2016	Small openings could contain some diverse bees but overall abundance may be low
Open pastureland and fields	Shelburne Farms, Shelburne, VT	Common	Bosworth 2016a and 2016b, Fowler 2016	Depending on mowing regime, bee diversity and abundance could be high
Recent timber harvest, large acreage, forest in early succession	Katahdin Woods and Waters National Monument, Patten, ME	Common	Fye 1972, Romey et al. 2007	Temporary, patchy habitat likely to benefit bees because of abundant flowers on early-successional plants
Sandy outwash plains	Kennebunk Plains, Kennebunk, Cumberland Co. ME; Wareham, MA	Local	Boulanger et al. 1967; Goldstein and Ascher 2016, Dibble et al. 2017	Unusual bee species might occur
Cranberry bogs	Southeast MA	Local	Mackenzie and Averill 1995, Loose et al. 2005	Extensive commercial bogs and also natural riparian habitats
Lowbush blueberry barrens	Blueberry Hill Farm, Jonesboro, ME (University of Maine)	Local	Bushmann and Drummond 2015, Venturini 2015 Drummond et al. 2017	On organic farms, moderate to good habitat; under intensive agriculture, pesticides could impact bee communities
Coastal islands and shores	Acadia National Park, Isle au Haut, ME; Martha's Vineyard, MA	Local	Goldstein and Ascher 2016, S.L. Bushmann unpublished data	Unusual bee species possible due to remoteness, possible separation from diseases and pests
Alpine zone	Mount Washington Auto Road, NH	Infrequent	Tucker and Rehan 2017	Unusual bee species might occur, not well-explored for bees
Wetlands, lakeshores, bogs, marshes	University of Massachusetts Cranberry Research Station, Wareham, MA	Common	Fowler 2016, Bushmann 2013	Perhaps low diversity but specialist bees possible
Small and large farms and orchards, diverse crops	Woodman Horticultural Research Farm, University of NH, Durham, NH	Local	Gabriel et al. 2010, Groff et al. 2016, Venturini 2015, Venturini et al. 2017a	Organic farms: good to excellent habitats for diverse bees. Farms might have under-recognized ground nest habitat and high bee diversity
Suburban parks, gardens, and remnant forest/field habitats	New England Wild Flower Society, Framingham, MA	Common	Fetridge et al. 2008, Lerman and Milam 2016	Habitat quality decreases if pesticides used and mowing is intensive. Might *Bombus affinis* be in city forests?
Urban parks and gardens	Portland Pollinator Partnership, https://portlandpollinators.org/ Portland, ME	Local	Hanley et al. 2014, MacIvor et al. 2014	Community awareness indicates quality of habitat could be increasing; *Bombus rufocinctus* may be possible.

Table 3. Continued

Habitat type	Example	Estimated abundance	Further information	Comments
Roadsides, highways, railroad corridors and utility corridors	Inquire of Departments of Transportation for a given state	Common	Hopwood 2013, Morón et al. 2014, Brianne DuClos, University of Maine, unpublished	May have good diversity where plant diversity is high, little or no herbicide used; remain alert for spread of invasive plants.
Closed landfills, reclaimed open-pit mines, other extreme land reclamation sites	Juniper Ridge Landfill, Old Town, ME	Local	Tarrant et al. 2013, Dibble et al. 2018, and F. A. Drummond. In press. Pollinator Habitat: A Cooperative Project Between the Landfill Industry and Blueberry Growers. Journal of Agricultural Extension and Rural Development	Could support unexpectedly high bee diversity.

then a grower might consider concentrating instead on another crop. To date, such an approach is rarely taken on a commercial scale. Even native crops like lowbush blueberry require regular interventions with pesticide to grow them profitably (G. Fish, Maine Department of Agriculture, Conservation and Forestry, Augusta, personal communication).

In agricultural systems, pesticides are stressors to bees that are compounded by other factors, such as lack of floral resources other than the crop, inadequate nest habitats for some kinds of bees, and other aspects not controlled by the farmer (Cresswell 2016). Bees on crop flowers commonly receive simultaneous exposure to multiple pesticide residues present in pollen (Drummond et al. 2012, Long and Krupke 2016, McArt et al. 2017, Mullin et al. 2010), and some of these combinations have synergistic negative effects on bees (Adler et al. 2016, Sgolastra et al. 2017). In NNE, field size of lowbush blueberries, highbush blueberries, apples, and squash tends to be small compared to agroecosystems of, for example, the Upper Midwestern and Western U.S. (USDA-NASS 2016), and this situation could provide wild bees with greater access to field edges, forest remnants, and other unsprayed habitats that might enable them to withstand some pesticide impacts.

The rise in demand for organic produce has led to a rapid increase across NNE in organic farms, as mentioned above, and this is a benefit to wild bee fauna. Certified organic growers can employ approved chemicals to control pests. Members of the public may be under the impression that organic means "no spray", but pyrethrins, spinosad®, a fungal biocontrol agent (*Beauveria bassiana*), sulfur, Bordeaux mixture, and some other allowable insect control methods are or can be highly toxic to bees depending on application methods, timing, and the species of bee exposed. Despite label warnings to apply when bees are not in the area, it is difficult to treat for pests or diseases when bees are not present on flowers, as many native bee species are active early and late in the day, and may sleep on flowers. Some organic growers in NNE refrain from using any toxic applications at all, thereby minimizing potential exposure of native bees to pesticide residues.

Since the mid-1980s, a minor revolution in pesticide use has taken place in NNE. DDT, carbamates and organophosphates were in popular usage by farmers in decades previous to that time; these were undeniably toxic to people, other mammals, birds, arthropod pests and beneficial insects. DDT was banned in the U.S.A. in 1972 for agricultural uses, though the Stockholm Convention on Persistent Organic Pollutants provided as of 2004 that DDT use is limited to vector (malaria) control. Aldicarb in the form of Temik®, a systemic carbamate, was used on the potato crop in the 1980s in northern ME; use in ME ceased in 2012, and the product will be phased out nationwide as of 2018. Such insecticides have been mostly replaced by use of pyrethroids (bifenthrin, permethrin, zeta-cypermethrin, lamba-cyhalothrin) or neonicotinoids (imidacloprid, clothianidin, acetamiprid, thiacloprid, nitenpyram, dinotefuran, and thiamethoxam). The neonicotinoids

are broad spectrum systemic neurotoxins that pervade not only the leaves, roots and fruits but the nectar and pollen of treated plants. Neonicotinoids are used to protect crops from biting and sucking insects such as thrips and aphids (Elbert et al. 2008, Cresswell et al. 2014). Imidacloprid was first introduced by Bayer CropScience in 1991 and in the years since, many more neonicotinoids have been developed and released onto the market. The neonicotinoids target the insect nicotinic acetylcholine receptor (nAChR) and are applied to the foliage, seed, or the soil. The crop plants take up the chemical, which is then distributed throughout the plant body (Elbert et al. 2008) including nectar and pollen, resulting in unintentional exposure of pollinators to neonicotinoids (Rortais et al. 2005, Cresswell et al. 2014).

Field-realistic levels of neonicotinoids in pollen and nectar may not cause significant direct mortality to pollinators. Lawrence et al. (2016) found that risk to honey bees at field-realistic levels is low. However, exposure to sub-lethal levels causes decline in colonies of honey bees regarding activity, fecundity, and foraging behavior and pathogen loads (Desneux et al. 2007, Laycock et al. 2012, Whitehorn et al. 2012). Disease can increase as a result of exposure to neonicotinoids (DiPrisco et al. 2013). In the United Kingdom over 18 years, bumble bees that foraged on oilseed rape flowers from neonicotinoid-treated seed had more population extinctions than those that foraged elsewhere (Woodcock et al. 2016). In Quebec and Ontario, bees picked up clothianidin in pollen from noncrop plants around corn fields in which the seed had been treated (Tsvetkov et al. 2017). Neonicotinoids may also have an effect on bee orientation. In a study conducted in MA, Averill (2011) treated *Bombus impatiens* workers from commercial colonies with topical imidacloprid and observed a significant effect of the treatment on the ability of the bees to navigate back to their colonies from 0.5 km away. Neonicotinoids are water soluble and have a half-life in soil, but this can vary from 200-1000 (+) days depending on the specific chemical, application method, and environment (Goulson 2013). The chemicals have potential to accumulate in the soil with successive applications. These systemic insecticides can remain within the plant tissue for over a year after application (Maus et al. 2005).

In Connecticut, Stoner and Eitzer (2012) examined pollen loads of honey bees and detected 60 different pesticides and metabolites. They found that when two neonicotinoids, imidacloprid and thiamethoxam, were applied to the soil of squash (*Cucurbita pepos* cultivars) the pesticides appeared in crop plant nectar and pollen at possibly sublethal concentrations. They recommended a revision in the method for quantifying pesticide toxicity in honey bee. Impacts upon smaller-bodied bees have not been measured but are thought to be proportionately greater as body size decreases. An investigation of wild bee communities in ME lowbush blueberry fields resulted in the finding that field management, which included neonicotinoid application (but at time intervals 12-22 months prior to bloom), did not significantly influence wild bee species diversity or abundance (Bushmann and Drummond 2015).

Production of conventional turfgrass relies upon pesticides to achieve a green, weed-free lawn. Alternative aesthetics and management styles are gaining popularity with the public in NNE. In Springfield, MA, a bee survey of 17 lawns over two years captured almost one-third of the state's recorded bee diversity, a total of 111 species (Lerman and Milam 2016). Results from similar studies in other parts of the world found that urban greenspace can support a surprising diversity of bees (Tommasi et al. 2004, Threlfall et al. 2015). The neonicotinoid class of insecticides, commonly used on lawns for grub control, is shown to harm *Bombus* spp. in suburban lawns, especially when applied as a dried powder (Gels et al. 2002). A mowing before chemicals are applied can reduce *Bombus* exposure to insecticides (Larson et al. 2013). Smaller bodied bees, more common in lawns (Lerman and Milam 2016), are likely to be even more severely affected by insecticide applications, depending on dose, due to the relatively higher concentration of toxin they receive relative to their body size. Imidacloprid applied to control grubs might be taken up by the fine root system of nearby shrubs, such as roses, that are eagerly visited by bees. The pollinators then are exposed to sublethal levels of insecticide in rose nectar and pollen over multiple seasons. Persistence of neonicotinoids and other products are covered by Bonmatin et al. (2015). In another example of an inadvertent impact, some recent products marketed to homeowners are intended to reduce tick populations by treating rodent hosts. Small amounts of pesticide-saturated nesting materials are made available and a rodent might take these into its burrow. After the burrow is abandoned, a non-target *Bombus* queen

(a)

(b)

(c)

(d)

Figure 3. Bee habitats in northern New England. (a) Research garden on an organic farm in Fairfax, VT where University of Vermont researchers studied the foraging preferences of pollinators on native herbaceous flowering species versus native cultivars (A. White photo); (b) Second-growth, closed canopy deciduous forest, near Downer Glen in White Mountain National Forest, Manchester, VT, Aug 19, 2013; (c) Coastal dune vegetation at Sandy Beach, W. Barnstable, MA (Cape Cod) adjacent to native cranberry bog habitat, Aug 18, 2016; (d) Alpine trail above treeline at Mt. Pierce, White Mountain National Forest, NH, Aug 16, 2012, elev. ca. 1150 m. (Photos by A. C. Dibble unless attributed otherwise.)

could attempt to nest there and be killed or weakened by the residual pesticide (Ginsberg et al. 2017).

Evidence mentioned here suggests that those installing pollinator plantings will want to source plant material that lacks pesticides. Even minute amounts of systemic insecticides could harm the same bees the plants are intended to support. The market in the region is already changing in response to public demand, as major retailers have begun marking plants treated with systemic pesticides. There are increasing options for obtaining organically grown seeds, seedlings, bulbs, and plants for the home garden, but better labeling of products is needed.

Only two statewide surveys of potential pesticide exposure in NNE (MA, ME) have been conducted (Lu et al. 2016, Drummond et al. 2018). The results of these surveys of pollen contamination suggest that there is high variation among sites within states and among states. More baseline data should be collected if we are to understand the potential exposure bees are experiencing in NNE.

Crop-associated habitat

Because bee-dependent crops are visited by both wild bees and managed bees, such crops as lowbush blueberry and cranberry are thought to exert a strong influence on habitat for wild bees in the vicinity of agricultural fields. Such fields are the best-documented among anthropogenic habitats in NNE. The four states produce the most lowbush blueberries, and a significant amount of cranberries (after Wisconsin) in the U.S., they host a robust economy of orchard crops, and they maintain other pollinator-dependent economies including bramble fruit, vegetable seed, flower seed, and cucurbit crops (e.g., squash and pumpkins). As honey bee colony regeneration costs escalate for beekeepers, pollination strategies may need to shift towards the enhancement of and increased reliance upon wild bees.

Mass flowering (the entire crop flowers briefly but simultaneously across the landscape for 2-3 weeks) overlaps with the active periods for many wild bee species. In lowbush blueberry, cranberry, and apple, wild bees have available an overabundance of pollen and nectar during crop bloom. For major pollinator dependent crops in NNE, crop areas, based on 2012 calculations (USDA NASS 2012), and time of flowering are as follows: (1) for lowbush blueberry in ME, about 7,329 ha for about three-four weeks in mid-May to mid-June, largely in Washington and Hancock Counties; (2) for cranberry in MA, 5,284 ha (in 2012) in June, primarily on or near Cape Cod; (3) for apple orchards in NH and VT, 1,233 ha, and in ME, 800 ha, in May; (4) for squash and pumpkin, over 2400 ha of fields across all four states in July-August. Additional crops also present forage resources for bees (Table 4).

Another pollinator dependent crop of NNE is apple, which is the largest pollinator dependent crop by area in NH and VT. Although we could find little information on bee communities in NNE apple orchards, nearby New York apple orchards host a diverse group of at least 104 species in 5 families (Gardner and Ascher 2006, Bartomeus et al. 2013b, Park et al. 2016). In these orchards, bees in the family Andrenidae are the most abundant and those in the Halictidae are the most diverse (Russo et al. 2015).

Additional important pollinator-dependent crops of NNE are pumpkins and squashes, which are largely pollinated by managed honey bees, bumble bees, and squash bees (*Peponapis pruinosa*) (Artz and Nault 2011, Stoner and Eitzer 2012). In some studies wild bee abundances are sufficient to meet crop pollination goals (Julier and Roulston 2009, Petersen et al. 2013), but see Artz and Nault (2011). Researchers in these studies concur that native pollinators significantly contribute to pumpkin and squash pollination, although in the short growing season of Ontario, Canada, the squash bee cannot be relied upon for commercial production because it is insufficiently synchronous with flowering period for those two crops (Willis and Kevan 1995).

A single crop can positively influence pollinator populations when it exists as a mass flowering component of a heterogeneous landscape (Diekötter et al. 2013, Holzschuh et al. 2013). Multiple mass flowering crops blooming in sequence within a landscape mitigate the pre/post-bloom dearth of resources often seen in agroecosystems that contain only a single mass flowering crop. In such systems, an initial buildup of bee abundance does not always result in population level increases (Westphal et al. 2008). Bee communities associated with an early mass flowering crop can exploit floral resources in nearby fields of other crops that bloom during the mid- or late-season, and this would support an abundant and diverse assemblage of bumble bees (Rao and Stephen 2010, Riedinger et al. 2013). In Europe, although mass flowering oilseed rape can boost the abundance of bumble bees (Westphal

et al. 2003), presence of crop bloom is associated with dispersion of bees across the landscape, reducing the pollination of native plants that co-flower with oilseed rape (Holzschuh et al. 2011).

Heterogeneous landscapes, where crops with complementary synchronous bloom phenologies are proximal to each other and within a matrix of natural habitat, could help balance effects of extreme floral abundance and can support wild bees (Rao and Stephen 2010, Reidinger et al. 2013). Co-flowering crop fields with little to no complementarity, e.g., field upon field of cranberry or lowbush blueberry, transform a landscape into a boom and bust cycle of pollen and nectar availability. This is seen as a disadvantage to wild bees, and contributes to grower reliance upon honey bee colony rental. Even intensively managed crops are expected to increase bee abundance when field size is small to moderate and seminatural habitats are present nearby (Winfree et al. 2007). In lowbush blueberry, wildflowers and/or weeds that grow along field edges provide season long floral resources for native wild bees. These floral resources appear to complement the floral resources of the mass flowering crop. Drummond et al. (2017) showed that abundance of native bees in lowbush blueberry fields were directly related to the abundance and richness of flowering non-crop plants growing along field edges. However, bee floral resources along field edges can also have undesirable effects, such as by serving as hosts for pest insects, as has been shown for the spotted wing drosophila in lowbush blueberry (Ballman and Drummond 2018).

Economics of managing bees and their habitats

The economics of managed bees have short- and long-term benefits and costs that vary according to the crop and the bee species involved. For example, cranberry, a native wetland plant of riparian areas, flowers in June and July. Though bumble bees are the most efficient pollinators due to buzz pollination and tongue-length (Averill et al. in press), honey bees are needed for crop areas that are unsustainably large because in this agroecosystem in MA, crop area is extensive and there is lack of habitat connectivity. The more habitat occupied by cranberry bog, the more rented honey bees need to be added and this can constitute 1.8% of variable operating costs (FCE 2010).

Producers and gardeners who grow lowbush blueberry, cranberry, apple, squash, and other pollinator dependent crops in NNE select pollination strategies best suited to their situations. These decisions require calculating the relative costs of using alternative pollinators (wild bees) as either direct substitutes for rented honey bees or as "pollination insurance." The annual costs per area of using pollination alternatives need to be balanced against the benefits of diversifying pollination sources as well as the amount of resources that producers, consumers, and society are willing to invest in wild bee conservation and alternative pollination options.

To decide whether to add bees to pollinate a crop, and how many to add, growers can select a method of monitoring bee abundance. For lowbush blueberry pollination services, see Yarborough and Drummond (2001); for crops, gardens, and natural areas, see Ward et al. (2014); and for natural areas and many other habitats, see Droege (2015). A combination of determining appropriate stocking densities of managed honey bees, with habitat management to favor wild bees, can optimize crop fruit set and yield as well as the production value of pollinator dependent crops in NNE.

Production value is the most cited valuation measure for pollination. Estimates of a crop's annual value, equal to crop price multiplied by total production, is adjusted by the dependence of a crop on pollinators, with evidence from crop fruit set, yields, and farm profits. The production value of pollination is the total crop value lost from a catastrophic collapse in crop pollinators. The costs of creating and conserving pollinator forage and habitat are part of this scenario; costs of pollinator conservation programs can be 20% of the production value of pollinator dependent crops (Breeze et al. 2014). This valuation measure may be less suitable for crops with lower or questionable dependence on pollinators such as soybeans (Melathopoulos et al. 2015). The measure may also overestimate pollination value in the long run where agricultural producers could adapt to shortages of rented honey bee hives through diversification into alternatives such as renting bumble bees (Stubbs and Drummond 2001, Drummond 2012) and creating habitats to amplify wild bee populations (Wratten et al. 2012, Blaauw and Isaacs 2014, Venturini et al. 2017b, Drummond et al. 2017).

Production value can be allocated between managed honey bees and wild bees based on the measured

or estimated contribution to crop pollination from these categories of pollinators. Across the U.S., crop production value for honey bees in 2004 dollars was estimated at $16.4 billion, averaging $5,296 per ha, while for wild bees this was $3.1 billion or $960 per ha (Southwick and Southwick 1992, Morse and Calderone 2000, Losey and Vaughan 2006). Within this context, the average production value for pollinator dependent crops in NNE in 2011-2013 (2012 dollars), for honey bees, totaled $268 million averaging $5,228 per ha. For wild bees the total was $72 million averaging $1,395 per ha (USDA NASS 2010-13).

Pollination production value estimates tend to exceed those for replacement cost, or the value of honey bee hives (supported by a particular habitat) that have to be regenerated to replace honey bee colonies lost to overwintering mortality, Varroa mite, or Colony Collapse Disorder. Across the U.S. in 2003, replacement cost of honey bee hives, assuming catastrophic collapse, was estimated at about $91.3 million (2,599,000 honey producing hives x $35.14/hive) (USDA NASS 2005, Rucker et al. 2012). Honey bee hive replacement costs in NNE pollinator dependent crops of lowbush blueberry, cranberry, pumpkins and winter squash are estimated at 3.1% of 2012 production value. This amounted to $10.4 million or $204 per ha of hive rentals (F.A. Drummond unpublished data; A. Jadczak, Maine Department of Agriculture, Conservation, and Forestry, personal communication). In comparison, at the national level, the U.S. replacement costs in pollinator dependent crops are estimated at $340 million or $7,384 per ha of crop production value (USDA NASS 2010-2013). Wild bees have not been included in replacement cost estimates because they are typically not transacted in formal markets (quads of *Bombus impatiens*, as managed bees, are an exception), and the cost of replacement is harder to quantify for wild bees.

Table 4. Northern New England crops that provide pollinator habitat. "ND" signifies that these data are not available.

Crop	Bloom	Pesticide application intensity	Pollinator dependency (0-1)[C]	# ha in MA[A]	# ha in ME[A]	# ha in NH[A]	# ha in VT[A]
Lowbush blueberry	mid-May to mid-June	low	1.0	145	15,631	236	15
Highbush blueberry	June to July[D]	medium	1.0	313	134	104	132
Cranberry	June to mid-July	medium	1.0	5,694	89	0	2
Raspberries[F]	June	medium	0.8	55	62	30	55
Blackberries, dewberries[F]	June	low	0.8	14	14	7	12
Apple	early May[D]	high	1.0	1,295	1,350	624	798
Cherries, all	May[D]	high	0.9	12	5	2	28
Peaches	early May[D]	medium	0.6	184	16	53	12
Pumpkin	July to August	high	0.9	750	260	246	251
Plums and prunes	early May[D]	medium	0.7	16	8	4	11
Squash	July to August	high	0.9	637	161	97	102
Other cucurbits[B]	late June to August	low	0.7-0.9	160	76	38	49
Strawberries	May to June[E]	medium	0.2	135	138	52	78
Vegetable seeds, all	varies by type	ND	1.0	1	26	ND	8
Flower seed	varies by type	low	ND	1	1	0	1
Sunflower seed	August to October[D]	ND	1.0	0	0	12	28

[A] Data from USDA Agricultural census (2012).
[B] Includes cucumbers, honeydew, cantaloupes, muskmelons, and watermelons. Pesticide application refers to cucumbers.
[C] Values from Morse and Calderone (2000) were derived and calculated from the literature and observations of Robinson et al. (1989). Range is 0-1.0, from no insect pollinator necessary for fruit set to total dependence on an insect for pollination.
[D] Exact bloom phenology varies by cultivar, but generally occurs within the time period shown.
[E] Bloom time is often controlled by the grower, but plants typically set fruit in mid spring.
[F] Listed in Morse and Calderone (2000) as brambleberry.

Production value estimates indirectly value the habitat required to support both managed and wild bees but do not measure the actual area of such habitat. One of the few studies to put a specific value on pollination contributed by a clearly defined area of surrounding natural habitat is Ricketts et al. (2004). They estimated the net increase in production value from 157 ha of forest parcels in 1 km buffers surrounding Costa Rican coffee to total $60,000 or $382 per ha.

The question of whether it is cost-effective to improve habitat for wild bees in NNE can be examined in several ways. Two approaches, production value and replacement cost, are often used but they do not capture the potential that improved pollinator habitat will increase abundance of managed and wild bees, nor do they include benefits from follow-on effects that could enhance farm productivity and profits. A more effective measure is the attributable net income, or the amount of net profit for a crop directly affected by bees, as proposed by Winfree et al. (2011). The measure is limited in NNE by the lack of quantification of managed and wild bee effects on pollinator dependent crop production and profits. For ME lowbush blueberry, a grower survey enabled assessment of the contribution of wild bees to fruit set in 1998-2012 (F.A. Drummond unpublished data). The attributable net income estimate valued honey bees at $2.16 million or $259 per ha, and wild bees at $1.44 million or $172 per ha. For MA cranberry in 2012, attributable net income estimates relied on grower surveys. Honey bees were valued at $1.68 million or $330 per ha, and wild bees at $0.88 million or $172 per ha (A. Hoshide unpublished data). Based on these estimates, attributable net income values of wild bee pollination services range from 52-67% of that for honey bee. This suggests that habitat improvement activities are worth time and investment to producers in NNE.

Pollinator habitat improvements include active and passive strategies. In a 2012 survey of 77 ME lowbush blueberry growers, active strategies such as planting bee pastures, owning honey bees, providing wild bee nesting materials, or renting bumble bee quads (Hanes et al. 2013) were employed by only 15-23% of participants. Passive strategies, such as recognizing minimally-managed areas and avoiding mowing wildflowers, altering pesticide use, and leaving standing deadwood, were employed by 55-68% of growers surveyed. Also in 2012 for 66 MA cranberry producers, 6-14% engaged in active strategies while 40-85% used passive strategies (A. Hoshide unpublished data). Another example of an active approach is to open the forest canopy, or feather the forest edge to make a finger-like configuration, and such areas within or at the edge of the woodlot provide natural regeneration of early successional plants visited by bees.

Costs vary for different aspects of improving pollinator habitat. The range in annual costs (including both fixed and variable costs) for minimal management of existing areas so that desirable bee forage will be maintained, versus, for example, planting pollinator pastures, is from $494 per ha for natural regeneration to about $2,000 per ha for planted pollinator pastures. This assumes a five-year stand life (Stevens et al. 2015) and can be up to 27% of NNE average production value per ha.

The rate at which active strategies for improving pollinator habitat find favor over passive approaches depends on the crop under consideration. In a 2013-2014 survey of 104 NH row crop growers of mostly annual pollinator dependent crops (e.g., winter squash, pumpkin, tomato, cucumber), L. Chute of Sullivan County Natural Resources, NH (personal communication) found that almost half of the respondents managed fields for connectivity of pollinator habitat. Half of these growers actively planted bee pastures, compared to only about 15% of lowbush blueberry growers in ME (Hanes et al. 2013) and cranberry growers in MA (A. Hoshide, unpublished data). Unlike annual crops, perennial berry crops (lowbush blueberry and cranberry) are not managed with cultivation equipment. Passive strategies such as reduced mowing of wildflowers were more common for these producers in ME (55%) and MA (40%).

Habitat improvements take up space that the crop might otherwise occupy, but no standardized ratio of pollinator habitat:crop has yet been proposed because conditions vary from one farm to another. Typically the area designated for pollinator habitat is smaller than the area occupied by cash crop(s). Blaauw and Isaacs (2014) found statistically significant fruit set and yield increases in Michigan highbush blueberry from pollinator plantings in a 1:27 ratio with the cash crop. In ME lowbush blueberry, Venturini et al. (2017b) found marginally significant impacts on fruit set from pollinator plantings in a 1:45 ratio to cash crop. At these ratios of pollinator plantings to crop, costs of planting pollinator pastures range from only $43.64 to $79.15

per ha of crop produced because the cost of pollinator pasture is covered by profits from the higher proportion of crop area.

Grower willingness to invest in wild bee forage and habitat enhancements may be insufficient in some parts of NNE. The costs of alternatives to renting honey bee hives not covered by state and government cost-share have to be paid by farmers, yet pollinator plantings can take 1-4 years to pay off (Blaauw and Isaacs 2014, Venturini et al. 2017b). Stevens et al. (2015) in a 2012-2013 survey of 80 ME lowbush blueberry producers and Hoshide in a survey of 66 MA cranberry producers (2013 unpublished data) found that the expense growers were willing to invest in such activities ranged from $175-$188 per ha per year. This does not cover the annual cost of $494 per ha to minimally manage land for native wildflowers by annual mowing, nor the costs of direct seeding bee pastures which can run up to $2,137 per ha (cost estimates include site preparation or maintenance, seed if planting, fixed cost of land as well as equipment depreciation). Can the marketplace cover these annual investment costs required for establishing floral resources for pollinators? Surveyed consumers of blueberries (including highbush) were willing to pay at least $0.51 per dry liter more for wild bee-pollinated blueberries, equivalent to $5,346 per ha (Stevens et al. 2015). As public awareness increases regarding the importance of wild bees in NNE, this willingness to help the grower pay for habitat improvements might increase also. Pressure for Farm Bill support for pollinator habitat enhancements could increase.

RECOMMENDATIONS FOR IMPROVING POLLINATOR HABITATS

In NNE the approaches to bee habitat improvements are based in part on nationwide practices (USDA NRCS 2009, Xerces 2012, 2015) with modifications based on reports or fact sheets published through University Cooperative Extension programs (Neal and Papineau 2015) and technical papers (Venturini et al. 2017a, Venturini et al. 2017b, Drummond et al. 2017, Rivernider et al. 2017). Demonstration gardens in NNE are available to the public and feature many of the aspects we mention in this article (Table 5). Upcoming publications will have direct applicability in the region (A.C. Dibble unpublished data, M.E. Leach unpublished data, L.L. Richardson unpublished data, A. White unpublished data).

Enhancement of existing bee habitat could be necessary in NNE because urbanization and intensive agriculture have altered habitat, and because an abundance of floral resources is perceived as scarce in some locales. Floral resources need to be pesticide-free, infrequently mowed, and with a succession of overlapping flowering periods on multiple plant species through the growing season. Small and large differences in pollinator habitat enhancement can have consequence for the bee community. There are roles for farmers but also for city planners, home gardeners, landscapers, greenhouse growers, park managers, departments of transportation, and landfill operators. We provide recommendations on how to improve pollinator habitat in NNE based on the literature and on our own experiences improving bee habitat across many sites (mostly on farms, landfills, and home gardens) in the region.

A conservation-oriented rule of thumb is to manage habitat for resilience (ability to recover after major disruption) while minimizing disturbance. In practice, however, most pollinator habitat management strategies in NNE focus on installation of plantings to increase floral resources as food for bees, so that pollination services on crops will be adequate. Perennial wildflowers of open habitats have been shown to attract pollinators, and their use in gardens is associated with an increase in bee abundance and diversity (Meek et al. 2002, Carvell et al. 2004, Pywell et al. 2005, Tuell et al. 2008, Blaauw and Isaacs 2014, Venturini et al. 2017a, b).

Soil disturbance is involved in planting new floral resources around farms, and this active approach might not be the best starting place. We suggest that first steps are to set goals, and these do not have to be exclusively about bee habitat as there are potential overlaps with entrepreneurial and ecological benefits (e.g., increase crop yield, protect biodiversity, improve early spring and late season floral resources, cultivate seed crops, cultivate cut flowers, cultivate culinary and medicinal herbs, cultivate plants with nutraceutical properties, improve and hold soil and prevent erosion by wind or water, reduce mowing frequency to save fuel and effort, offer demonstration gardens from which others can learn, and not least, improve aesthetic aspects around the farm or property by retaining diverse vegetation at field edges or by planting pollinator strips). If the goal is to increase bee populations, this is worthwhile

but difficult to measure because bee abundance fluctuates from year to year, both in short term (1-4 years, Bushmann and Drummond 2015) and long-term (29 years, Drummond et al. 2017) time horizons, so it may be challenging to track changes.

In an iterative process with setting goals, it is important to assess existing habitat features in a walk-around survey during good weather in the growing season. A bee monitoring protocol can be employed (see sources above). A full-scale bee inventory is probably not realistic, but representative information and highlights with photos can be used to acquaint the landowner with some of the common species and their habitat needs. This passive approach is effective and cost-saving as a starting place because planting — which is expensive — may be unnecessary, and vulnerable habitat elements such as a bee nest in the ground might be recognized and worked around. It is possible that reduced mowing, minimization of pesticides, and feathering the edge of a woodlot (explained above) could accomplish much toward meeting goals.

Site characteristics are unique to a given location. Among the features to recognize are the amount of sunlight available, which affects potential for plantings. Soil type and soil drainage properties, slope, and aspect have implications for ground nesting bees. Native plant communities may be present, or field edges could have invasive plants that need control. Bloom phenology will be apparent in one or a few visits, as will some of the common bees indicative of the bee community. Can a potential gap in the flowering season be detected? Consider not only the herb and shrub layer but trees, including willows, maples, shadbush, cherries, and basswood. On a more refined level, it might be possible to assess floral resources in terms of corolla-length as long- and short-tongued bees might be accommodated purposefully. Weed pressure could constrain pollinator plantings, or perhaps there is a cover crop already in place that functions as a floral resource (Venturini et al. 2017b). Another aspect to notice is proximity of a woodlot with large dead trees and logs (bee nesting and overwintering substrates).

Baseline conditions shaped by management affect pollinator habitat enhancement. Mowing intensity, burning practices, crop rotation, intensive forest harvest, and pesticide use each represent a management area where modifications could lead to bee habitat improvements. Factors to regard when assessing pesticide use include: which pests are problematic, what pesticides are applied, and how often? Perhaps the landowner is already using Integrated Pest Management strategies, or could be interested in alternatives less toxic to bees. Pesticide drift is an issue, and might originate in a neighbor's field. A buffer could help protect from pesticide drift, depending on its width. Effectiveness could depend on substance toxicity, concentration, application method, and droplet size. Access for planting activities, including a set-up for watering, will improve chances of success in a bee pasture. If a farm has an area around buildings that is not exposed to pesticides, this could be an appropriate place for increasing floral resources.

Stemming from the passive approach, practical habitat improvements have been undertaken by some growers in NNE recently. One approach is to establish a refugium for honey bee hives and existing floral resources, within which pesticide drift is unlikely, e.g., near house and barns, or around a water supply. It is easy enough to mow less frequently (see Milam et al., in press, and Lerman et al. 2018) and with the blade set higher. It might be possible to reduce and minimize herbicide treatments. Where possible, recognize bare patches of soil that might already be occupied by ground-nesting bees. In forest operations, to promote native bee nesting leave standing dead trees in the woodlot unless they present a safety hazard. As much as feasible, promote pithy-stemmed shrubs such as elderberry, raspberry, blackberry, and sumac.

It may become apparent that additional floral resources are needed to meet the objectives for habitat improvements, so a more active approach, such as establishing a pollinator meadow, could be used in combination with aspects of the passive approach. Site preparation is crucial; a site with minimal weeds will better assure success of an expensive seed mix. Organic growers usually do not have the option of herbicides, and mechanical control methods could be preferable in any regard. Weed control may take 1-2 growing seasons to accomplish, depending on conditions. For larger areas, repeated shallow tillage, or tillage plus cover crops can be used to control competing vegetation. Time of sowing may depend on location and on the seed supplier's directions, and can be spring, autumn, or on top of the snow (see demonstration gardens at University of New Hampshire). Sow by hand broadcasting, mechanical drop seeders, or no-till seed drills. To assure

contact with the soil, roll the newly sown site with a weighted barrel. Once the planting has germinated, additional weed control may be needed at some sites. This may include hand weeding, spot treatment with herbicides, or even a grass selective herbicide if grass weeds are a problem.

A mowing regime has many possibilities for improving floral resources for bees, as mown areas often include not only wind-pollinated grasses that sometimes provide bee forage (Rivernider et al. 2017), but diverse herbs that flower and attract bees such as dandelion, white clover (can flower when lawns are mowed above 6.3 cm or 2.5 inches), creeping thyme, or creeping Charlie (*Glechoma hederacea*). Whether the area is in lawn or fields, timing and cutting height can be adjusted to favor flower abundance. Where practical, managers can refrain from mowing a field that is full of dandelions or other flowers (unless seeking to control an invasive plant such as tall lupine by reducing seed production), and can wait for a lull in the flowering periods of the plants in that field. If close mowing is needed, the area can be divided into sections and mowed in alternating weeks. Cover crops can be considered for a larger area. Some can be considered in a rotation, e.g., buckwheat (*Fagopyrum esculentum*), bee's friend (*Phacelia tanacetifolia*), borage (*Borago officinalis*), and clovers (*Trifolium* spp., *Lotus corniculatus*, *Melilotus* spp., *Medicago*, *Vicia*, etc.). A few of these would be appropriate for a small-scale pollinator garden (borage, bee's friend) but most are too rangy in habit, or spread, and are not recommended for any but a meadow-type planting.

Clovers are not native in NNE, but they represent a mainstay in some pollinator plantings because most of them are easily grown, seed may be inexpensive, they have a relatively long flowering season, and long-tongue bees visit them readily. They may enhance forage that will enable honey bees to build up the winter honey supply, and are likely to be visited by bumble bees. Clovers are favored by hunters who plant food plots for white-tailed deer in the region, and are purposely introduced into gaps and small clearings deep in the forest. Tucker and Rehan (2016) used a bipartite visitation network to visualize a plant-pollinator community in NH. Red clover (*Trifolium pratense*) was visited by the greatest richness of bee species (20 of the 118 species detected). White clover (*T. repens*) was visited by the greatest abundance of pollinators (primarily *Bombus impatiens*); this was more than twice the number of bees found on flowers of any other plant species. Clovers also emerged as an important food source in a comparison of bee pastures in the margins of ME lowbush blueberry (Venturini et al. 2017b). *Melilotus officinalis* and *T. pratense* were visited by an abundance of social bees (*Bombus* spp. and *A. mellifera*), while a wildflower mix attracted a greater diversity, mostly solitary Halictidae. Venturini et al. (2017b) also found that small areas of bee pasture installed in lowbush blueberry cropland provided 37% of the pollen collected by *Bombus* spp. and slightly improved fruit set of the crop. Regarding birdsfoot trefoil (*Lotus corniculatus*), data from four ME farms in a common garden study (A.C. Dibble et al. unpublished data) plus anecdotal observations along roadsides in ME suggest this plant attracts Megachilids in midsummer and could be a valuable plant to support that group of bees. Unlike those species mentioned above, crown vetch (*Coronilla varia*) appears to not attract many bees, and is used to hold soil by departments of transportation in NNE.

Hay fields can be managed to support honey bees. There is need for development of hay mixtures and management strategies that promote legume floral development. Preliminary research in VT demonstrated that adding an appropriate cultivar of white clover with alfalfa provided bloom from June through mid-September (Bosworth 2016a, 2016b). Other legumes such as red clover and birdsfoot trefoil could also be used to support native bees. Timing of mowing for the hay crop is important to enhance flower abundance. The challenge for hay management is balancing between pollinator services by allowing the crop to go to bloom, verses crop quality for livestock by cutting early.

Bee habitat enhancements include considerations of nest habitats. For ground-nesting bees (e.g., *Andrena, Colletes*, some Halictidae), mounding of earth to form a well-drained south-facing berm could encourage ground-nesting bees to colonize in that spot. This was tried in ME on an informal basis but bee colonization was inconclusive. In some parts of ME, over-use of herbicide to favor the lowbush blueberry crop at the expense of weed diversity and abundance has benefited bees by leaving patches of ground unvegetated, and some of these bare soil patches became occupied by ground-nesting bees. For construction of artificial nest blocks for *Megachile* and *Osmia*, hole dimensions vary by bee size. Plans are in Stubbs and Coverstone (2004), available at http://umaine.edu/publications/7153e/).

Table 5. List of demonstration pollinator gardens in northern New England. All have public access, safe parking off the road, some interpretive materials available, and may have tours offered. See web sites or ask contacts for updated information regarding each.

Site name	Address	Contact information
Garland Farm	475 Bay View Dr., Bar Harbor, ME 04609	www.beatrixfarrandsociety.org. Signage, self-guided tours, scheduled events may be available.
YardScaping Gardens	Back Cove, Portland, ME	Contact Gary Fish, State Horticulturist, Maine Department of Agriculture, Conservation and Forestry gary.fish@maine.gov, 207-287-7545
University of New Hampshire Woodman Research Farm	70 Spinney Lane, Durham NH 03824	Contact Dr. Cathy Neal, UNH Cooperative Extension cathy.neal@unh.edu, 603-862-3208
Blueberry Hill Farm, University of Maine	1643 US-1, Jonesboro, ME 04648	Contact Superintendent Blueberry Hill Farm, University of Maine, 207-434-2291
University of Vermont Horticulture Research and Education Center	65 Green Mountain Dr., South Burlington, VT 05403	Contact Dr. Terry Bradshaw, University of Vermont, Terence.Bradshaw@uvm.edu, (802) 658-9166 http://www.uvm.edu/~hortfarm/
Pollinator Garden	University of Massachusetts Amherst	Contact Jarrod Fowler (jarrodfowler@gmail.com) or Dr. Anne Averill (averill@eco.umass.edu)

Recommendations vary as to whether to treat the wood used in construction of artificial nests with any preservative or sealant, including paint. Condensation and undue moisture might increase likelihood that fungus will compromise soil- and stick-nesting bee brood. It may be necessary to protect the blocks from bluejays and woodpeckers. For stem-nesting bees (e.g., *Ceratina*), grow elderberry, raspberry, blackberry, and sumac. Nests for bees that prefer hollow stems can be made by tying together bundles of stems of these plants and suspending them under an eave of an outbuilding, although it has been observed that this type of nest might facilitate parasitoids of bee larvae (Drummond, personal observation). For bumble bees, planting of bunch grasses is recommended with the intent that the bumble bees could eventually occupy old mouse nests at the base of a clump of bunch grass. Species suggested for this include: tufted hairgrass (*Deschampsia flexuosa*), deertongue (*Dichanthelium clandestinum*), false melic (*Schizachne purpurascens*), and little bluestem (*Schizachyrium scoparium*), all of which are native in NNE. Several introduced species are also suggested: orchardgrass (*Dactylis glomerata*), purple moor grass (*Molinea caerulea*), sheep fescue (*Festuca rubra*), and timothy (*Phleum pretense*). A native sedge, wool-grass (*Scirpus cyperinus*), is in some lists. Some of these plants might be weedy competition for crops such as lowbush blueberry, and may not be appropriate in all situations.

Along with all these considerations, there may be opportunities to improve habitat connectivity by recognizing bee resources in the vicinity of the property in question. Those who prioritize protection of bee habitat might coordinate with other parties to recognize and improve a pollinator habitat corridor that will increase sustainability of the habitat improvements and benefit other kinds of wildlife. Such a corridor, especially in an urban area, may need vigilance regarding encroachment by invasive plants, but has the prospect of multiple uses for recreation and as green space, in addition to goals regarding bee habitat.

Installation of additional floral resources may be needed to improve pollinator habitat; if so, it is important to use plant species that have a high visitation rate by bees (suggestions in Table 2). Not just any flowering plant will do. Until recently, plant lists for NNE pollinator habitats have included anecdotal evidence and recommendations from other regions. New data from NNE can enable managers to improve pollinator habitat specific to the region (Fowler 2016, Neal and Papineau 2015, Venturini et al. 2015, Venturini et al. 2017b, White 2016). Bees require floral resources through

the entire growing season, though for some bees their individual life span might be just three weeks. To support bee communities, the Xerces Society and NRCS recommend that at least three plant species that bees visit are in flower at any one point during the growing season ("early", "mid", "late"). Indeed, more than 12 plant species might be required to meet this challenge because (1) the only plants relevant are those that attract bees; (2) plant species reported to attract bees in other regions might not elicit similar responses in NNE; and (3) some plants are short-lived or succumb to competition from others after a few years. Use of native species and local ecotypes of native plants are desirable if available. Flowering period for the added plants should either overlap the bloom period of the crop, or avoid competing with it, depending on preferences of the grower.

Plant selection is an aspect of bee conservation that the public finds compelling, and from which the green industry (landscape designers and garden centers) can profit given widespread interest in pollinator plantings. Seeds and nursery stock that are local genotypes are ideal, with no recent systemic pesticide treatment. It might be practical to try to plant for specialist bees, within various other constraints. By meeting needs of specialist bees, the generalist bees are likely to be accommodated also (Fowler 2016). This might be particularly conducive if a wetland is available, as some specialist bees associate with obligate wetland plants (Giles and Ascher 2006).

Some examples of native plants that are visited by wild bees include those mentioned above such as willows (*Salix* spp.), goldenrod (*Euthamia*, *Solidago*), aster (*Doellingeria, Eurybia, Oclemena, Symphyotrichum*), and milkweed (*Asclepias*), and there are many more (Table 2.) A trend toward planting native plants in the region is laudable but for the sake of bees, not all plants in the garden must be native. Native plants, especially woody species, are essential to development of Lepidopteran larvae that are food for birds (Tallamy 2007), but native plants as the sole components of a bee garden, in some situations, may be limiting with some gaps in availability of flowers during periods in the growing season. Introduced, noninvasive plants can be a mainstay of pollen and nectar for honey bees and wild bees during times in the growing season when relatively few native plants are in flower, such as mid July into about mid-August. Introduced plants may be crucial to meeting management goals such as supporting honey bees on a farm. Some of these plants persist on their own but do not take over natural areas. These can be cost-effective, reliable, and rewarding in their long bloom season, wildlife uses, soil holding capabilities, and other aesthetics; some may be valuable food or seed crops for commerce. Table 2 includes examples that may fit with other management goals.

Plants that flower extremely early or late in the season are limited among native species, but with addition of non-native species, forage during these two shoulder seasons can be improved. Examples of introduced plants for early spring from ME are Crocus (*Crocus vernum*), cross-leaved heath (*Erica tetralix*) for early spring in a rock garden situation, and Japanese pussy willow (*Salix chaenomeloides*), which flowers before most native willows. Plants that continue flowering after most native asters and goldenrods have gone to seed are the bottle gentians (e.g., *Gentiana andrewsii, G. clausa*), which are visited by *Bombus* into mid October or later in ME.

When planted as part of a cropping system, wildflower plantings should not include plants that serve as alternative hosts to crop pests. For example, members of the Rosaceae (shadbush, chokecherry, wild cherries, quince) might attract Japanese beetle and stem borers, or otherwise increase problems in association with the crop. Willows provide early season bee food but are also a host plant for numerous Lepidopterans, most of which are native and benign, but others may be considered pests. These types of considerations could be pointed out to farmers and orchardists seeking to reduce their use of pesticides.

A native but weedy plant such as common milkweed (*Asclepias syriaca*) is eagerly visited by bees and other pollinators, and is a host plant to the Monarch butterfly. Though it spreads, it might be provided with places here and there that are out of the way or that can be mowed in autumn after seeds have dispersed. In some situations, its value to beneficial insects may outweigh the costs of its weediness. A native weedy plant presents far different challenges than an invasive plant such as tall lupine, which has come to dominate roadsides in ME and elsewhere, and reduces area occupied by native milkweed due to its early spring growth and dense shade at the soil. Milkweed emerges after many native herbs, and certainly much later than tall lupine, so is out-competed for light, space, nutrients and moisture.

In summary, bee habitat improvements may indeed involve plantings but it is wise to first recognize vulnerable features that might already be used by bees and protect those if possible. A passive approach could save money and time, and facilitate meeting goals. When plantings are undertaken, the plants selected ought to provide a succession of flowers over the growing season. They might be used to meet multiple objectives in addition to bee forage. Native plants and local genotypes might be prioritized but many introduced, non-native plants could also be highly useful, depending on the goals for the project.

GAPS IN KNOWLEDGE

We identified areas for which research is lacking and that we think need added attention in coming years. Tier 1 items are those that could have implications for pollination security and bee conservation, and Tier 2 items are important also but are less obvious in their direct benefits for people.

Tier 1

- Impacts of climate change need to be assessed regarding pollinator habitat and bees. The drought of 2016 in NNE is an example of weather patterns that could be more frequent in coming decades. An advantage could go to long-tongue bees because nectar flow is low during drought but long-tongue bees (some *Bombus*) can meet their nutritional requirements more easily than short-tongue bees.
- Competition at flowers between wild bees and managed bees is not yet quantified in NNE. Are diseases and pests being transmitted from honey bee to wild bees in the region, from managed *Bombus* to wild *Bombus,* or from introduced *Osmia* to wild *Osmia* species?
- Bees can transmit parasites and pathogens at flowers, but the role of different plant species in transmission is largely unknown. Two papers have shown that transmission of bee pathogens (*Crithidia, Nosema*, and *Apicystis*) between bumble bees or honey bees differs between two flowering plant species (Durrer and Schmid-Hempel 1994, Graystock et al. 2015), and one study found differences in *Crithidia* transmission to bumble bees across 14 plant species (Adler et al., in review). However, we still largely do not know the role that plant communities play in transmission of bee parasites and pathogens.
- Sources are needed for locally grown seeds and plants that are local genotypes, true wild types, and free of systemic pesticides.
- While many plant lists can be found to improve pollinator habitat, there are hundreds of plants — native and introduced — that could potentially function well in pollinator plantings but have not yet been assessed. Needed are data regarding which plants do well in the region and are valuable to bees. Bee nutrition has been studied for only a few plants, and much more data are needed regarding the relative qualities of plants for bee nutrition. Effective plant lists for NNE must be based upon data and not so much on anecdotal evidence or proxies from other regions.
- Native plants are not well documented regarding the bee species that visit them, or regarding the extent to which they depend on insect pollinators. Which bee species depend on certain plants? Where specialization does occur, there could be less resilience to environmental changes.
- If pollinator habitats are created especially for bees and other pollinators, will the populations of these animals increase as a result? It is unknown whether higher bee abundance, due to presence of pollinator plantings, increases likelihood of disease and predation but there is a possibility that density dependence could lead to fluctuation of bee abundances. Better methods for determining bee community dynamics are needed, studying one species at a time is not a promising approach, although it can provide important insight into mechanisms affecting changes in bee species abundance.
- There is need in NNE for data to support selection of seed sources of wild types; a fledgling cottage industry of local-sourced seed purveyors has yet to achieve much market share but could emerge over time.
- Host plants associated with oligolectic bees might include rare or declining plants in NNE. This needs

further investigation and strategies for reversing decline.

Tier 2

- The role of the municipality and the county could be better outlined as these two layers of government play a role in pollinator habitat improvement. Municipalities such as Portland, ME (G. Fish, personal communication) are taking the lead in new efforts to establish pollinator corridors that will benefit other wildlife in addition to pollinators. They may be able to help agencies incentivize and enable small businesses that provide seeds and plants for pollinator habitat. Also, municipalities may be responsible for aerial spray programs to control insect-vectored diseases, and such spray could impact pollinators.
- If climate change continues to bring more wet weather during the spring growing season, or hotter summers in the Northeast, then some bee species could be adversely affected because they might be unable to complete their life cycles. Bees that fly in spring could be particularly vulnerable as spring seasons in recent years have started early, then turned cool and wet compared to historic trends.
- Measures to protect bees from pesticides and to provide more floral resources and nest habitats could likely lead to small, localized increases in some bee populations, depending on the bee species. But there could be a concentration of bees in which pests and pathogens are shared at a higher probability than if bee gardens and nest habitats are not improved. This needs quantification.
- What are the differences between qualities of pollen and nectar of invasive plants compared to those in native plants and "benign" introduced plants that are popular in bee gardens?
- How species-specific are kleptoparasites? If wild bees are in decline, then this might impact the kleptoparasites that rely upon them and this would have detrimental consequences for biodiversity.
- Can ground nest habitats be created for solitary bees, and how best to do this? If this piece can be put in place, then farmers and gardeners could move bees where they want them, reduce exposure to pesticides, and perhaps build up populations.
- Given the likely increase in variability of weather patterns, and of rainy weather during spring, what habitat modifications might be made to increase likelihood that bees can complete their life cycles?
- Can a network of demonstration pollinator plantings be expanded and improved to meet the needs of farmers and the public?
- Testing of seed mixes could focus on these qualities in pollinator plantings: they attract pollinators, remain low and dense so do not require mowing, harbor few or no insect pests, and are relatively nonflammable. Such mixes are needed for potential use along railroad rights of way, roadsides, and highways.

In conclusion, we suggest that the public's interest in improving pollinator habitat is likely to continue to grow. Habitats in NNE include many patches of native vegetation, but some of this is closed canopy forest that is not likely to support abundant wild bees because of lack of flowers at some points during the growing season. Invasive plants are expanding their populations rapidly in the region and need to be controlled early and often, regardless of the floral resources some of these species offer to bees. So far there are few data by which the nectar and pollen of such plants can be assessed. Threats due to increased variability in weather, including more wet weather in spring, could mean that some early bees are unable to provision sufficient brood, but this is not yet well-quantified. In all, bees of NNE remain incompletely known. Habitat improvements are an appropriate emphasis, but use of passive approaches can save resources and protect features that already function to support bees. With excellent site preparation and continued management, pollinator plantings can play an important role in pollinator-dependent cropping systems and in pollinator conservation efforts, but these will probably need to be replanted periodically.

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